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THE ANCYLIDAE OF LAKE OCHRID AND THEIR BEARING ON INTRALACUSTRINE SPECIATION

BY

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[Accepted 10th February 1959]

(With 4 plates and 25 figures in the text)

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INTRODUCTION

It is a well-known fact that the faunas of the few ancient lakes of the world are characterised by a high degree of endemism. This can, *a priori*, be explained in two different ways. The endemic faunas may be relict faunas, remnants of older faunas, or their endemic character may be due to evolution within the lakes. Although there was formerly a tendency to emphasize the first explanation, the modern view leans towards the second. Brooks (1950), Greenwood (1951), and Hubendick (1952) have independently described the possible way of intralacustrine speciation in ancient lakes. According to these authors isolation between populations is considered in principal to be of the same basic importance in intralacustrine speciation as in speciation in general.

Concerning the comparatively small and unitary Lake Ochrid in the Balkan Peninsula, Brooks writes : " The general features of the vertical distribution of the members of some (species) flocks are known and have been indicated, but the horizontal distribution has never been investigated for any, making it impossible even to hazard a guess about the nature of the geographical barriers involved ". A study of the Ancylidae of Lake Ochrid, undertaken by me, reveals some interesting features which permit certain probable conclusions regarding speciation within the lake.

Lake Ochrid was visited by me during August and September, 1957. The visit was undertaken with the aid of grants from the Royal Swedish Academy of Science and the foundation Lars Hiertas Minne. The studies were carried out with the Hydrobiological Station, Ochrid, as a base. Boats and collecting

gear were there freely put at the author's disposal, who wishes to express his gratitude to Professor S. Stanković, founder of the station, and to Dr J. Sapkarev, director of the station ; he is also much indebted to Dr P. Radoman and Mr S. Hadžišče, both of whom helped significantly with collecting.

REVIEW OF THE ENDEMIC ANCYLIDAE OF LAKE OCHRID

ANCYLUS TAPIRULUS Polinski, 1929

A. tapirulus lives normally on shells of dead or live specimens of *Dreissena polymorpha* (Pallas). These shells predominate in the bottom material in the depth zone between about 18 and 35 meters. Within this zone the occurrence of the populations of *A. tapirulus* is found. Abundant material of the species was obtained.

The shell. (Pl. 1, Figs. 1–4). The circumference of the shell, i.e. its aperture, is largely elliptical with a length/breadth ratio between 1·20 and 1·32. In adult shells the length of the aperture can exceed 5·5 millimeter but is most commonly between 3·0 and 4·8. The breadth of the aperture reaches about 4·0–4·5 millimeter and the shell height as much as 3 mm. but is generally less. The entire shell length, with the apical region included, can reach 6 mm. but in full-grown specimens seldom exceeds the length of the aperture.

The ellipticity of the aperture is not always quite regular. Occasionally the broadest point is anterior or posterior to the middle of the aperture and, accordingly, the posterior or the anterior end respectively is more pointed than the opposite end.

Along the peristome or the edge of the shell the periostracum extends about 0·1 mm. beyond the calcareous shell border. (Pl. 1, figs. 2–3, *p.*) ; its periostracum is yellowish brown and cracks and falls off when the shell gets dry.

The apical region is cornet-shaped and slender. In young specimens it is pointed more or less posteriad and downwards, in adult shells more ventrad. In young shells the projection of the apex always falls posterior to the base of the shell, in adult shells it generally falls inside the base. The apical region often shows a slight deviation towards the right, or sometimes to the left. The tip of the apex is blunt and smooth. The rest of the apical region is longitudinally or axially striated with about 20 to 25 fine striae. In adult shells the striae are often worn and difficult to trace.

The apical region is usually delimited from the rest of the shell by a furrow or constriction. Sometimes there is a distinct growth line at the limit of the apical region, and this can take the form of a narrow eaves-like projection around the shell. Occasionally a similar formation can occur further down on the shell, and below this formation there may be a small concavity in the shell.

Below the apical region the shell forms a convex slope anteriorly and laterally. The slope is less steep anteriorly but the steepness increases gradually posteriad on the lateral sides. Posteriorly, below the apex, the shell may be perpendicular to the base or even concave.

Below the apical region the shell surface is almost smooth and an extremely fine concentric growth sculpture occurs, but is hard to observe even at a magnification of fifty times.

External pigmentation. If scattered pigment dots on the head and sides are disregarded, the pigmentation is limited to the dorsal side of the visceral mass inside an unpigmented zone along the mantle border. This zone is generally broader in *A. tapirulus* than in *A. scalariformis* and *A. lapicidus.* (see below). Between this zone and the shell adductors there is dense black or dark gray pigmentation. Anteriorly between the ends of the shell adductor the corresponding pigment zone is often—but not always—considerably paler. Above the adductor and more centrally the pigmentation is paler and fades slowly towards the usually unpigmented apical region. Except in the darkest pigmented areas the pigment is arranged in a cellular pattern with lacunae corresponding to the nuclei, and usually also to cell borders. In the most densely pigmented zone the pigmentation may show a tendency of being radiary arranged. The pigment is black.

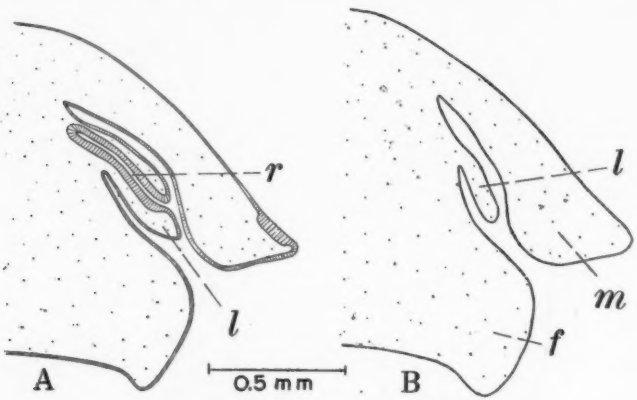

Fig. 1.—*Ancylus tapirulus.* Outline of cross section through left half of body at the anal pore (A), and behind the anal pore (B). Frontal view.
f, foot ; *l*, lateral flap or pseudobranch ; *m*. mantle border, *r*, rectum.

External shape of animal. The front of the head is very bluntly rounded. Its ventral side with the mouth, is semilunular in shape. The relaxed sole of the foot is regularly elliptical. The tentacles are situated just behind and dorsal to the eyes. They reach only a little in front of the head. They taper gradually but are not sharply pointed. The maximum breadth of the mantle border is slightly less than half the breadth of the sole. It is broadest laterally and tapers posteriad, slightly also anteriad. Below the small rest of a mantle cavity is an unfolded lateral flap, the pseudobranch (Pl. 1, fig. 3 ; text-fig. 1). Its anterior portion is slender but becomes broader posteriorly. The rectum

runs through the flap to the anus, which is located terminally on it. Below the middle portion of the pseudobranch is the female genital pore. The male genital pore is situated just behind the left tentacle.

General internal organisation. The general internal organisation pattern is to a certain extent dependent on the form of the whole animal. In *Ancylus* two features are of special importance namely, the reduction of the visceral hump and its spiral form, and the strong development of the foot with its adductor muscle system. Owing to these features a relatively limited space is left for the viscera as compared with related gastropods such as *Lymnaea* and planorbids. Apart from what there is in the head the viscera must be lodged in the bowl-shaped space formed by the musculature of the foot and the adductor muscles (Fig. 2). The " bowl " is open anteriorly below the laminate dorsal muscle under a strip of adhesive epithelium which forms an apparent anterior junction between the antero-lateral ends of the adductor. The muscular bowl is also open on the middle section of its left side and the rudimentary

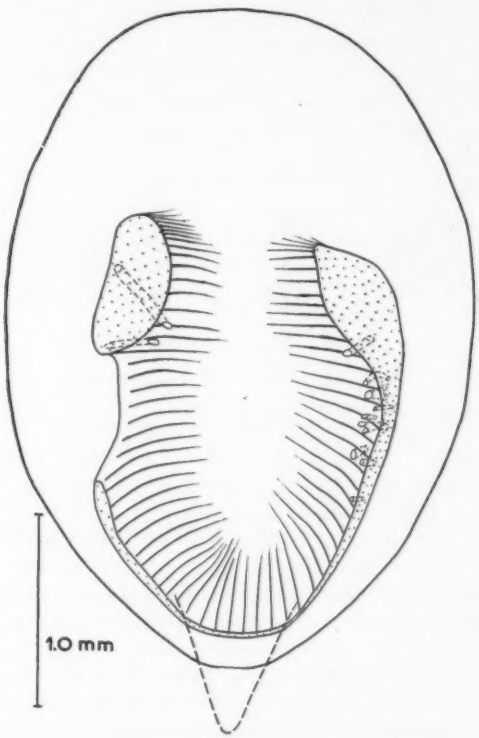

Fig. 2.—*Ancylus tapirulus*. Diagram of the shell adductor muscle system. Dorsal view. Dotted areas indicate dorsal attachment surfaces of adductor muscle. The larger canals for nerves and blood lacunae are indicated by thin broken lines.

mantle cavity opens through this interspace. The rectum and the female gonoduct also reach the body wall through the same opening in the muscular " bowl ". Numerous narrow canals also penetrate the wall of the " bowl ", giving space for blood lacunae and nerves.

The left and right anterior parts of the adductor muscle are strongest. Its right lateral and its posterior parts are also strong although comparatively thin. The muscles continue down through the sole where they partly cross over to the opposite side.

In most Basommatophora there is a well-developed mantle cavity. Certain organs, such as pericardium, kidney and at least part of the vascular system of the lung are as a rule located in the ceiling of the mantle cavity. The floor of the cavity consists normally of a thin membrane called the diaphragm. In *Ancylus* (Fig. 3) where the mantle cavity is almost non-existent, the pericardium

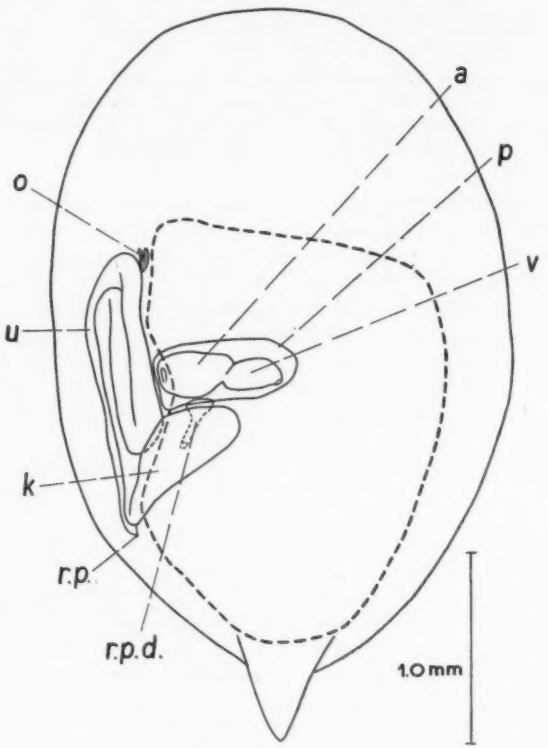

Fig. 3.—*Ancylus tapirulus*. Diagram of the pallial organs in dorsal view. The thick broken line indicates inner limit of furrow between mantle border and rest of body. The slight inwards bend of this line indicates the rudimentary mantle cavity.

a, atrium ; *k*, kidney proper ; *o*, osphradium ; *p*, pericard ; *r.p.*, renal pore ; *r.p.d.*, reno-pericardial duct ; *u*, urethra ; *v*, ventricle.

rests directly on the visceral organs and a diaphragm does not exist, though the ventral wall of the pericardium may be regarded as functionally corresponding to part of the diaphragm.

In connexion with the reduction of the mantle cavity the kidney has been displaced to the left mantle border (Fig. 3). Only a part of its most proximal portion is still inside the muscular " bowl ". It passes out through the opening on the left side.

In the Lymnaeidae and Planorbidae for example the viscera are located in two large haemocoeles, the visceral and the cephalic haemocoele. These

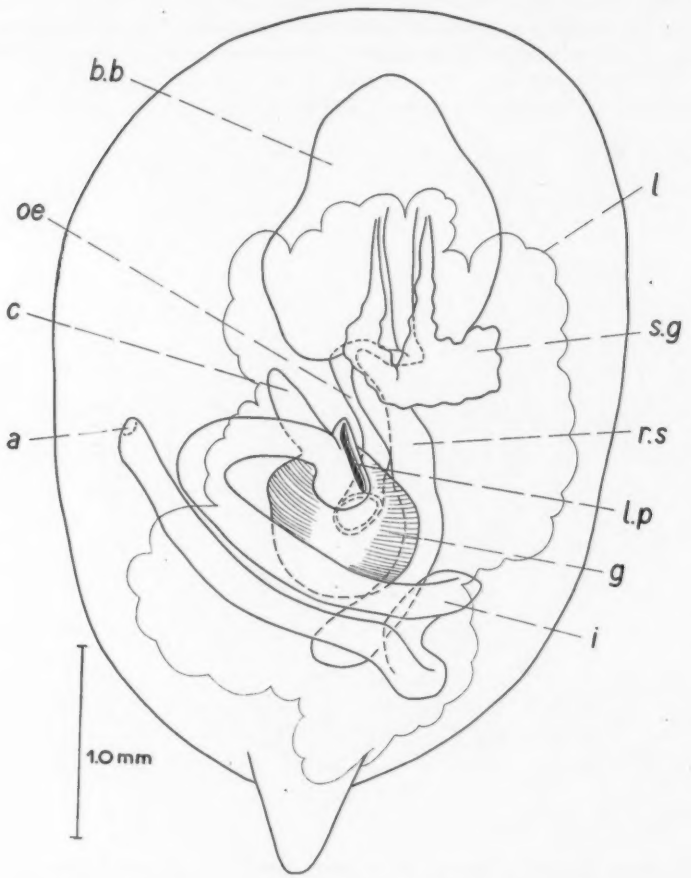

Fig. 4.—*Ancylus tapirulus*. Diagram of the alimentary system in dorsal view. *a*, anus ; *b.b.*, buccal bulb ; *c*, caecum ; *g*, gizzard ; *i*, intestine ; *l*, contour of the liver *l.p.*, liver pore ; *oe*, oesophagus ; *r.s.*, radula sac ; *s.g*, salivary gland.

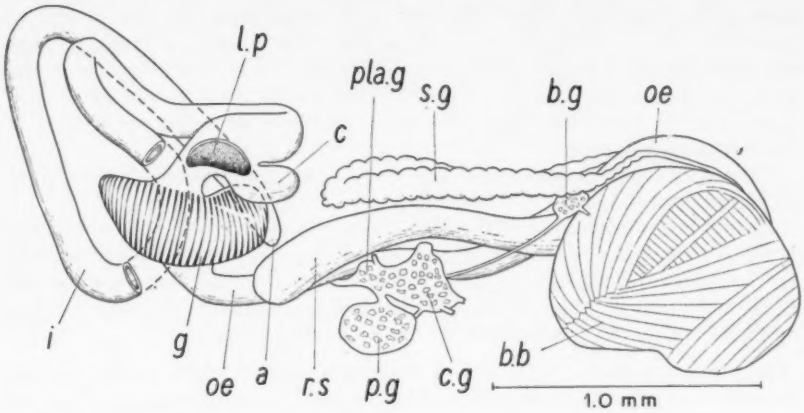

Fig. 5.—*Ancylus tapirulus*. Diagram of alimentary system with liver removed, viewed from the right. The muscles of buccal bulb are stylized.
b.g, buccal ganglion ; *c.g*, cerebral ganglion ; *p.g*, pedal ganglion ; *pla.g*, pleuroparietal ganglion. Other lettering as in Fig. 4.

are incompletely separated from each other by the cervical septum (a term introduced by Carriker, 1947) ; this septum does not occur in Ancylidae. In the Lymnaeidae, for example, the anterior part of the cephalic haemocoele, where the buccal mass is located, is screened from the remainder of the haemocoele by a thin connective tissue membrane, the capitocerebral membrane. It has not been possible to detect such a membrane in *Ancylus*. Only one large haemocoel surrounding practically all the viscera seems to be present. This viscero-cephalic haemocoel is connected with blood lacunae in the mantle border, the pseudobranch and the foot. Except in the neighbourhood of the pericardium and in the long cephalic aorta, true blood vessels do not occur. The cephalic aorta empties into a lacuna between muscles of the ventral side of the buccal bulb.

The pallial organs. As already mentioned, the mantle cavity is almost completely reduced (Fig. 3). The left end of the pericardium is situated above the small remnant of the cavity. The whole thin-walled pericardium reaches across the left half of the body and is located immediately below the dorsal body wall. The comparatively large, thin-walled atrium is to the left, and the smaller, more muscular ventricle to the right in the pericardium. The aorta leaves the latter ventro-posteriorly near the median line of the body.

In the posterior wall of the pericardium there is a funnel-shaped bulge or excavation merging into a narrow tube with ciliated walls. This is the relatively long reno-pericardial duct, which leads to the sac-like upper part of the kidney. This is the main excretory part of the kidney, but a considerable part of the long serpentine renal duct is also excretory in function. The excretory epithelium reaches to the middle of the second, or posteriorly directed

part of the first renal loop. The rest of the renal duct, the last portion of the first loop and the whole second loop, forms the ureter. It opens through the very narrow excretory pore on the inside of the left mantle border in the posterior third of the body. With the exception of the proximal sac-shaped portion of the excretory system the whole kidney and uretha are located in the left mantle border.

The whole mantle border is richly vascularised and is probably important as a respiratory organ.

In the mantle border, not far from the most anterior turn of the urethra, is the osphradium or Lacaze's organ. It is formed as a small invagination in the inside wall of the mantle border near the junction between this and the bulk of the body. The invagination has, besides its sensory elements, ciliated epithelial cells and is surrounded by the osphradial ganglion.

The alimentary system. The mouth with an arcuate jaw (Pl. 1, Fig. 5) leads into the lumen of the well developed buccal bulb. The radula sac is long and reaches far back through the ventral part of the visceral mass (Figs. 4 and 5). The salivary ducts enter the buccal bulb on either side of the oesophagus. The glands are joined behind and thus form a U-shaped unit. None of the glands pass through the cerebral ring. The oesophagus begins antero-dorsally on the buccal bulb, runs ventrad behind the bulb, through the cerebral ring, and further posteriad to the ventral side of the gizzard, where it enters the latter. The intestine goes out from the pyloric part of the stomach, which branches off a caecum, resembling a style-sac. In the same region the liver is connected with the pylorus part through a large pore. The intestine forms two loops before it runs across the body to the anal pore distally on the pseudobranch. The digestive gland occupies to a great extent the dorsal part of the visceral mass.

Histological studies need not be made in this study. The morphology of the jaw and the radula however, need some further comments.

The jaw (Fig. 6) consists of a slender dorso-median section and two more prominent lateral sections. All sections are built up of chitinous bars, each consisting of a variable number (from 3 to about 15) of phalanges. Each phalanx is a dense bundle of extremely fine thread-like structures. The phalanges of one bar are arranged more or less like roof tiles. The bars, and to some extent also the phalanges, are only loosely connected to each other.

The radula (Fig. 7) is simple with all teeth unicuspid. The cusps are slightly pointed but have blunt, rounded tips. In the marginal teeth the rudimentary cusps may be sharper. In a full grown specimen the number of teeth per cross row is about 31 to 35.

The central nervous system (Fig. 8) has large cerebral ganglia without any protruding dorsal lobes. The most lateral main nerve (to tentacles and eyes) from each cerebral ganglion goes out from a laterally projecting part of the ganglion. The pedal ganglia are connected with each other through a pedal and a slender and more posteriorly located parapedal commissure. The right pleural ganglion is incorporated in the right parietal ganglion. On the left side, there is a small vestige of a pleural ganglion. It is well delimited from

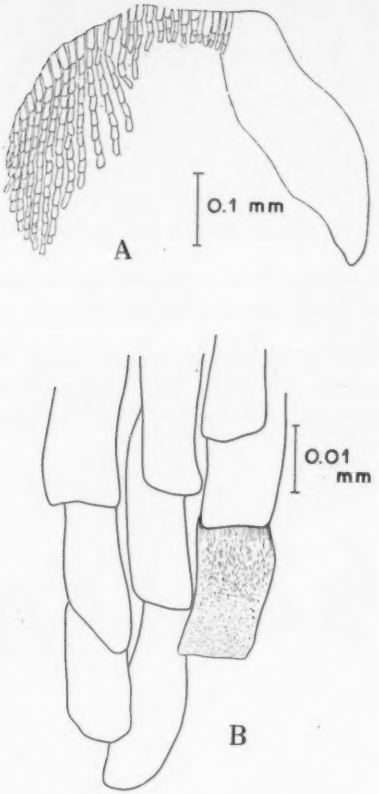

Fig. 6.—*Ancylus tapirulus*. Diagram of the jaw (A) and of a few phalanges of the jaw (B). Frontal view.

the pedal ganglion, but there is no distinct delimination between this rudimentary ganglion, on the one hand, and the left parietal and left cerebral ganglia on the other hand. Apart from the parietal ganglia there is only one ganglion in the visceral commissure.

Reproductive system. The gonad is located in the posterior region of the visceral mass (Fig. 9). It consists of six to ten rather thick acini. A short serpentine duct connects it with the thin-walled and irregularly shaped vesicula seminalis. From this the hermaphrodite duct leads to the carrefour where it branches into the oviduct and sperm duct. The albumen gland joins the system through the carrefour. The albumen gland is small in the figured specimen, but can sometimes have a considerable size, occupying a large part of the space in the visceral mass. The oviduct merges into the comparatively

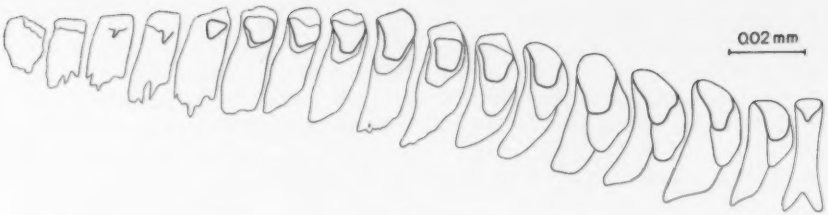

Fig. 7.—*Ancylus tapirulus*. Diagram of half a cross row from the radula in dorsal view.

large uterine gland complex, which, after joining the spermathecal duct leads to the vagina and the female pore. The spermatheca is pear-shaped and of about the same length as its duct.

The sperm duct leads to the prostate which consists of a few comparatively large diverticula (Fig. 10). There can be as few as two diverticula, branched or unbranched. From the prostate the vas deferens runs in a loop through the

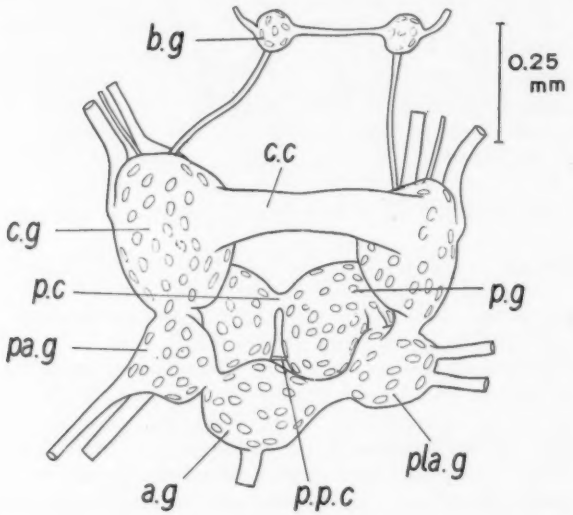

Fig. 8.—*Ancylus tapirulus*. Diagram of central nervous system in dorsal view. *a.g*, abdominal ganglion ; *b.g*, buccal ganglion ; *c.c*, cerebral commissure ; *c.g*, cerebral ganglion ; *p.c*, pedal commissure ; *p.g.*, pedal ganglion ; *pa.g*, parietal ganglion ; *pla.g*, pleuroparietal ganglion ; *p.p.c*, para pedal commissure.

subdermal region outside the left anterior portion of the shell adductor to the male copulatory organ (Fig. 11). The latter consists of a large thin-walled preputium. The small penis sheath is normally partly invaginated in the upper portion of the preputium. The duct from the long glandular flagellum

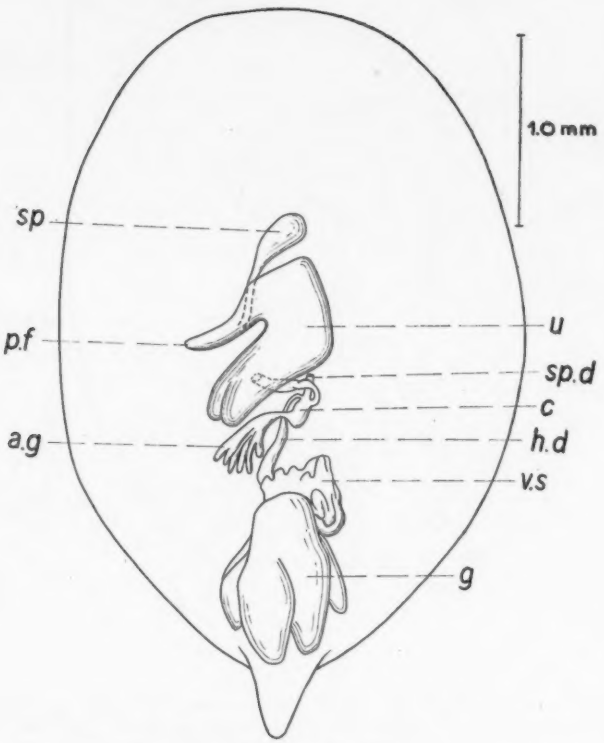

Fig. 9.—*Ancylus tapirulus*. Hermaphrodite and female parts of reproductive system, the organs are slightly separated. Dorsal view.

a.g, albumen gland ; *c*, carrefour ; *g*, gonad ; *h.d*, hermaphrodite duct ; *p.f*, female genital pore ; *sp*, spermatheca ; *sp.d*, sperm duct ; *u*, uterine gland complex ; *v.s*, vesicula seminalis.

enters the copulatory organ proper close to the invaginated connexion between the vas deferens and the penis sheath. The lowest part of the flagellar duct also participates in the invagination into the preputium. The flagellar duct widens distally and opens into the lower end of the penis sheath. The latter is comparatively slender. The penis has a lateral pore and lacks distal armament. In the preputium there are two longitudinal folds which divide the lumen into two chambers. The pendant complex of penis sheath and distal end of flagellar duct fills up most of the larger chamber. The other chamber has a comparatively narrow lumen.

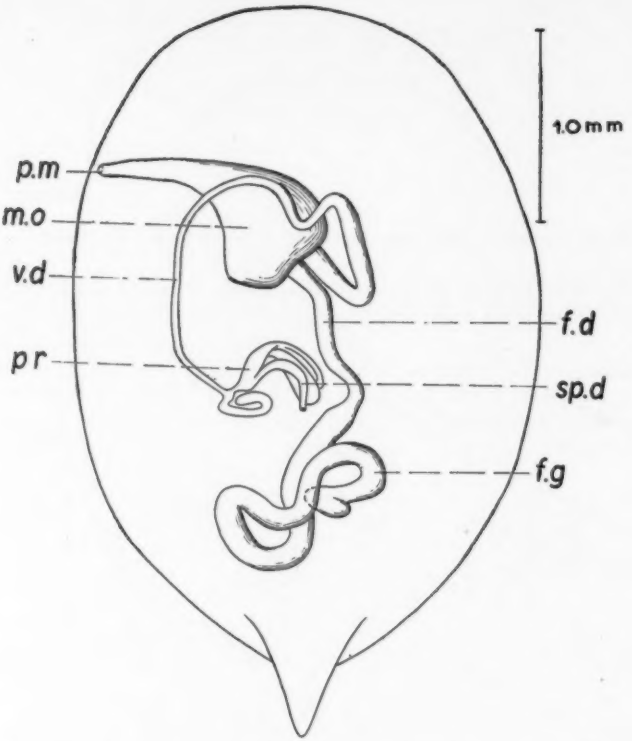

Fig. 10.—*Ancylus tapirulus*. Male parts of reproductive system in dorsal view. *f.d*, flagellum duct ; *f.g*, flagellum gland ; *m.o*, male copulatory organ ; *p.m*, male genital pore ; *pr*, prostate ; *sp.d*, sperm duct ; *v.d*, vas deferens.

ANCYLUS SCALARIFORMIS Stanković & Radoman, 1953

A. scalariformis lives on the same substratum, i.e., shells of *Dreissena*, and in the same zone (i.e. the so-called shell zone between about 18 and 35 metres depth) as *A. tapirulus*. Stanković & Radoman (1953) state that *A. scalariformis* does not occur together with *A. tapirulus*. However, in the dredgings in 1957 the two species were found together. Stanković & Radoman also mention that they found some young shells of *A. scalariformis* on littoral stones at a depth of one metre at the eastern shore of the lake. Probably these specimens belong to another species, *A. lapicidus*, which will be described below.

Abundant material of *A. scalariformis* was obtained.

The shell. (Pl. 1, fig. 6 ; Pl. 2, figs. 1–3). The circumference of the shell, i.e., the aperture, is almost regularly elliptical with only small aberrations. The length/breadth ratio of the aperture is between 1·05 and 1·27, thus

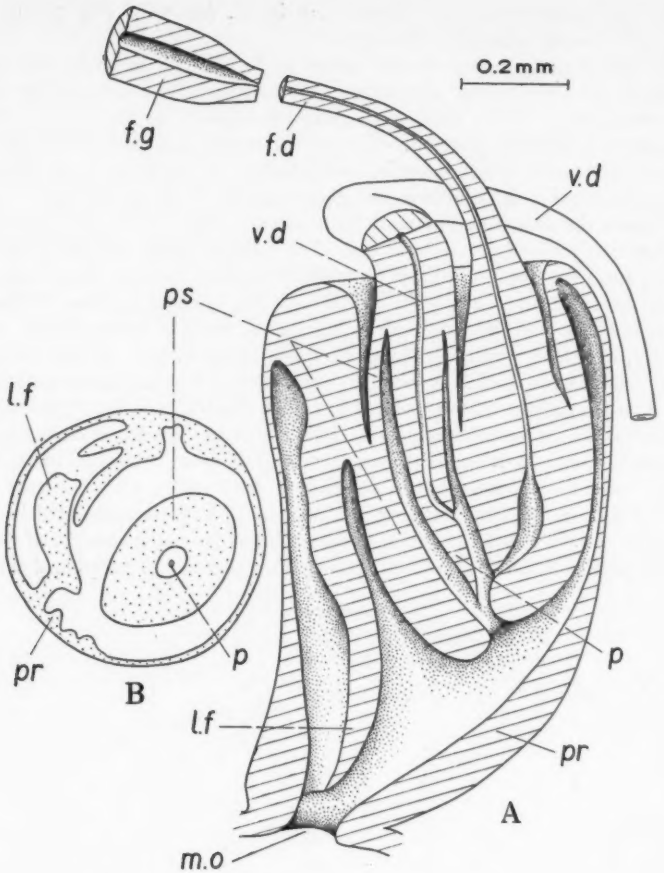

Fig. 11.—*Ancylus tapirulus*. Stereogram of longitudinally-sectioned male copulatory organ (A) and diagram of slightly less enlarged cross section through the same organ at the lower end of the penis (B).

f.d, flagellum duct ; *f.g*, flagellum gland ; *l.f*, longitudinal preputial fold ; *p*, penis ; *pr*, preputial wall ; *p.s*, penis sheath ; *v.d*, vas deferens.

the aperture of *A. scalariformis* tends to be slightly rounder than in *A. tapirulus*. The length of the aperture may reach 6 mm. but is generally between 3·5 and 5·5 mm. The breadth of the aperture reaches about 4·6 mm. and the shell height seldom exceeds 3·0 mm. When the apical region is included the shell length generally exceeds that of the aperture with 0·2 mm. in adult specimens.

The thin, pale-brown periostracum extends between 0·10 and 0·15 mm.

outside the calcareous shell border. As in *A. tapirulus* the periostracum becomes deformed when the shell dries.

The cornet-shaped and slender apical region points more or less directly posteriorly in very young specimens and almost directly ventrally in full-grown specimens. It is median or deviates slightly to the right. The tip of the apex is bluntly pointed. The apical region has about 20 axial striae but these are more or less worn in adult shells. In such shells the projection of the apical region falls outside the posterior end of the aperture.

Between the apical region and the aperture there are a varying number of eaves-like projections around the shell ; their width increases with their distance from the apex. Although generally convex on their dorsal side, these projections are bent dorsally in relation to the general outline of the shell. Immediately below the projections the shell surface often slopes steeply ventrally, and then again continues at a less steep angle. If the projections are left out of consideration, the shell surface thus becomes more or less step-like. The animal itself too can have a similar slip-like profile. The eaves-like outgrowths are narrower than in *A. lapicidus* (see below), seldom exceeding in width 10 per cent of the shell length ; their number seldom exceeds four.

The connexion between the eaves-like outgrowths and the rest of the shell has been studied by grinding sections through shells embedded in plastic (Fig. 12). It appeared that each outgrowth has been the margin of the shell during a period of the snail's life. After such a period the peripheral continua-

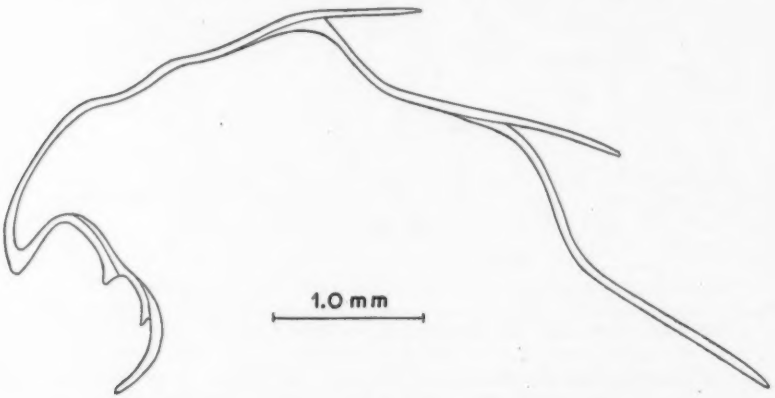

Fig. 12.—*Ancylus scalariformis*. Diagram of longitudinal section through shell, seen from the right.

tion of the growing shell has begun a certain distance inside its shell margin, thus leaving this margin as an eaves-like projection.

The main outline of the shell is similar to that in *A. tapirulus* but is, as a rule, slightly flatter.

Apart from the eaves-like outgrowths there is no shell sculpture and, hardly any visible microscopic sculpture, except in the apical region.

Fig. 13.—*Ancylus scalariformis*. Diagram of half a cross row from the radula in dorsal view.

External pigmentation. The ventral side of foot and head, the lips, the tentacles and a peripheral zone of the mantle border lack pigmentation. Between the unpigmented mantle border zone and the adductor muscle area there is a zone with dense pigmentation. This zone is especially broad anteriorly between the dominating antero-lateral parts of the shell adductor. In this area the pigmentation shows a tendency to be radially orientated. Above the shell adductors, and on the whole central part of the animal, there is a less dense pigmentation, mostly with a cellular pattern (i.e., the pigmentation is arranged in accordance with the epithelial cells). Lacunae in the pigmentation correspond to cell borders and nuclei. The mesh size in this cellular pattern is about 0·02 mm. All external pigmentation is gray or black.

External shape of the animal. This is similar to that of *A. tapirulus*.

Internal anatomy. In *A. scalariformis* the internal anatomy is identical with that in *A. tapirulus*. The only organ in which slight differences between the species can be expected is the radula. However, even the radula of the two species is almost identical. In *A. scalariformis* (Fig. 13) there are a few additional marginal teeth due to the slightly larger size of this species.

ANCYLUS LAPICIDUS sp. n.

Eight specimens of this species were found in the shore zone at the middle part of the wastern side of Lake Ochrid which is built up of limestone. They lived on the under side of loose limstone rocks about 30 to 50 cm. below the water surface.

The shell. (Pl. 2, figs. 4–6 ; Pl. 3, figs. 1–3). The aperture is almost regularly elliptical with a length/breadth ratio varying between at least 1·02 and 1·25. The shell is comparatively small, it reaches 2·5 mm. in length, 1·85 mm. in breadth and 0·95 mm. in height in the material available. The species may reach a larger size as the specimens studied were not mature.

The apical region is cornet-shaped but proportionately broader than in *A. tapirulus* and *A. scalariformis*. It has about 20 distinct longitudinal or axial ridges. In the lower and broader portion of the apical region additional finer ridges can occur between the dominating main ridges. An extremely fine transverse sculpture can occur between the ridges in the same part of the apical region. A similar growth sculpture is sometimes also visible just below the eaves-like outgrowths.

As in *A. scalariformis*, there are a varying number of concentric eaves-like outgrowths between the apical region and the aperture. The outgrowths are comparatively broad and can exceed 15 per cent of the shell length and in every projection the periostracum extends beyond the calcarous shell material. The projections can be rather densely located and a shell of 2·5 mm. length may have 5 projections.

The main outline of the shell below the apical region is rather similar to that of *A. tapirulus* and *A. scalariformis*. As in the latter species, the eaves-like outgrowths interrupt the principal outline of the shell, but in a different way. The projections are slightly concave dorsally. Thus they diverge from

the main surface of the shell without causing the latter to bend steeply downwards below the outgrowths. Consequently the shell and animal do not have a step-like profile.

The periostracum, that projects beyond the shell margin, is transparent and colourless.

External pigmentation. The darkest external pigmentation is located just lateral to the adductor muscle region but fades gradually and terminates just dorsally of the mantle border. This pigmentation is indistinctly radially arranged. The pigmented area contains a large number of irregularly arranged, unpigmented dots. This arrangement seems to correspond to a cellular pattern where the nuclei correspond to the unpigmented dots but where cell borders are not distinctly marked in the pigmentation. Dorsally to the adductor muscles the pigmentation is extremely weak or almost non-existing. All pigmentation has a reddish-brown tint.

External shape of the animal. The general dorsal profile of the animal forms an even curved line and not a wavy outline as in *A. scalariformis*. The external features of *A. lapicidus* are otherwise similar to those of *A. tapirulus* and *A. scalariformis*.

Internal anatomy. The few specimens available of *A. lapicidus* does not permit a thorough anatomical examination of the species. However, no major differences from the other species of *Ancylus* of Lake Ochrid have been noticed. Aphalie does occur. The radula is of the same general type as in *A. tapirulus* and *A. scalariformis* but is smaller and has considerably fewer lateral teeth (Fig. 17).

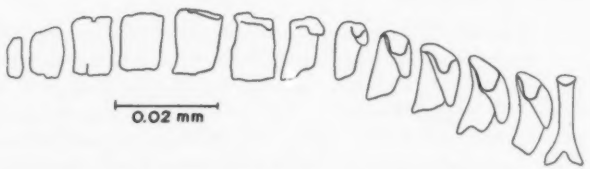

Fig. 14.—*Ancylus lapicidus*. Diagram of half a cross row from the radula in dorsal view.

Differential diagnosis. Ancylus lapicidus is similar only to *A. scalariformis* but in the following characteristics differs from the latter. When the eaves-like projections are disregarded, the surface of shell (and animal) is even, not step-shaped as in *A. scalariformis*. The shell is smaller, the apical region tapers faster and is blunter. The latter points more directly posteriorly than in *A. scalariformis* (where it points more or less ventrally). The apical region has a stronger radial sculpture than in *A. scalariformis*, and, in addition, there are traces of a transversal sculpture. The eaves-like outgrowths are proportionately broader than in *A. scalariformis*, and their breadth sometimes exceeding 15 per cent of the shell length. The periostracum is paler than in *A. scalariformis*, and the dermal pigment is reddish brown, not grey or black. The radula has fewer lateral teeth than in the closely related species.

The holotype has been deposited in the Naturhistoriska Riksmuseum, Stockholm, number 1922.

ACROLOXUS IMPROVISUS Polinski 1929

Acroloxus improvisus lives mainly on shells of dead and living *Dreissena polymorpha* (Pallas), which predominate in the sub-littoral zone between about 18 and 35 metres depth, i.e. in the same environment as *Ancylus tapirulus* and *A. scalariformis*. Numerous specimens were obtained.

The shell. (Pl. 3, figs. 4 and 5 ; Pl. 4, fig. 1). The form of the circumference of the shell or its aperture varies. The anterior half of the shell is normally symmetrical whereas its posterior part is slightly asymmetrical, its posterior tip being located to the right of the median line. Sometimes also the anterior end is asymmetrical, its tip being located to the left of the median line, this giving the whole shell the appearance of a parallelogram. As a rule the broadest part of the shell is anterior to its middle. The shell length of adult specimens is usually between 3 and 4 mm., the maximum breadth is between 2 and 2·5 mm., and the height between 0·9 and 1·4 mm. The length-breadth ratio is normally between 1·4 and 1·5, length-height ratio between 3·1 and 3·4.

The apical region is pointed and turned to the left at an angle of between 30 and 45 degrees from posteriad direction. In addition, the apex is normally bent more or less ventrally. The apical region has an extremely fine longitudinal striation with about 30 striae. The connexion between the apical region and the rest of the shell is often marked by a slight concavity. Below this follows, anteriorly and laterally, a smooth convex shell. The periostracum reaches beyond the edge of the calcareous shell all around the aperture. The shell is practically colourless.

External pigmentation. Immediately outside the adhesive epithelium areas and the upper surfaces of the adductor muscles (the latter structures are to a large extent, but not throughout, covered by the former) is a dark grey-pigmented zone. The pigmentation fades gradually in a peripheral direction. To the inside of these structures there is a less dense pigmentation, also grey in colour. The pigmentation has a cellular pattern where unpigmented areas correspond to cell borders and nuclei.

External shape of animal. The general form of the body corresponds of course to that of the shell. The head is short and blunt frontally. The tentacles are slender but blunt. The foot is more or less eliptical. The eaves-like mantle border is well-developed all around the animal. Below the aperture to the rudimentary mantle cavity the right body wall forms a blunt process through which the female pore opens. This process is continued posteriorly becoming gradually more and more sharply ridge-shaped. The anal pore opens through its edge. Behind the anus the ridge has the form of a thin flap which is not folded but sometimes has an uneven surface. The whole structure is the mantle flap or mantle lobe or pseudobranch.

General internal organisation. As in *Ancylus* the visceral hump and its spiral form are reduced, and the adductor muscle strongly developed in *Acroloxus*.

As a consequence similar displacements of the viscera have taken place. There is, however, one major difference in the general organisation between *Ancylus* and *Acroloxus*. In *Acroloxus* the whole anatomy is reversed compared with *Ancylus*, the opening of the rudimentary mantle cavity, the anus, the genital pores, the osphradium, the kidney, and the pseudobranch being located on the right side instead of on the left. Another difference is the separation of two rather well-delimited haemocoels.

As in *Ancylus* a cervical septum is lacking. Unlike *Ancylus*, however, a capitocerebral membrane is present. This screens off the anterior part of the viscero-cephalic haemocoele, forming a special buccal haemocoele. This surrounds the buccal bulb. The cephalic aorta leads blood directly to this

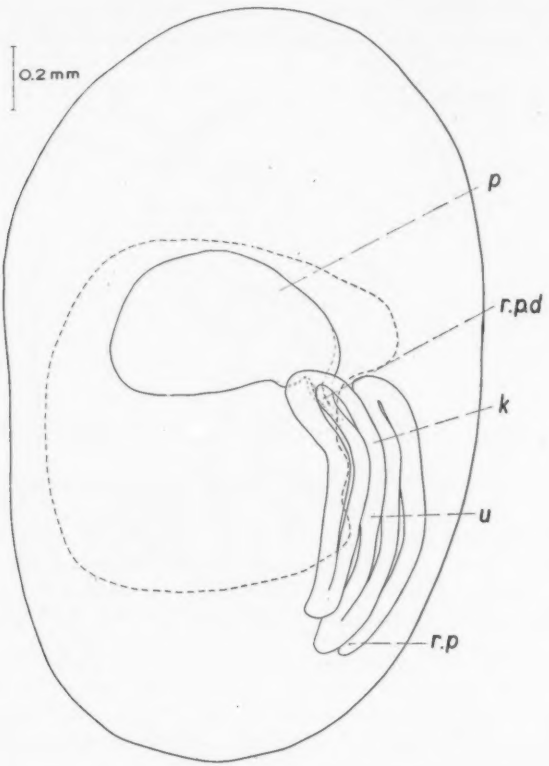

Fig. 15.—*Acroloxus improvisus*. Diagram of pericardium and excretory system ; the thicker broken line indicates the inner limit of the furrow between mantle border and the rest of body. The inward bend on the right side marks the rudimentary pallial cavity.
k, kidney ; *p*, pericardium ; *r.p*, renal pore ; *r.p.d*, reno-pericardial duct ; *u*, urethra.

buccal haemocoele. The rest of the viscero-cephalic haemocoele is connected with other parts of the body through blood lacunae in a similar way to that of *Ancylus*.

Pallial organs. As in *Ancylus*, the pallial cavity is reduced and has the form of the shallow depression in the right side behind the right anterior adductor muscle. In the under side of the mantle border, immediately anterior to the mantle opening, is the osphradium ; it is of the same type as in *Ancylus*.

The pericardium (Fig. 15) is centrally placed on the dorsal side of the animal. The heart has the atrium to the right of the ventricle. The reno-pericardial pore is located in the right posterior corner of the pericardium. The reno-pericardial pore and the first portion of the renal tube are provided with

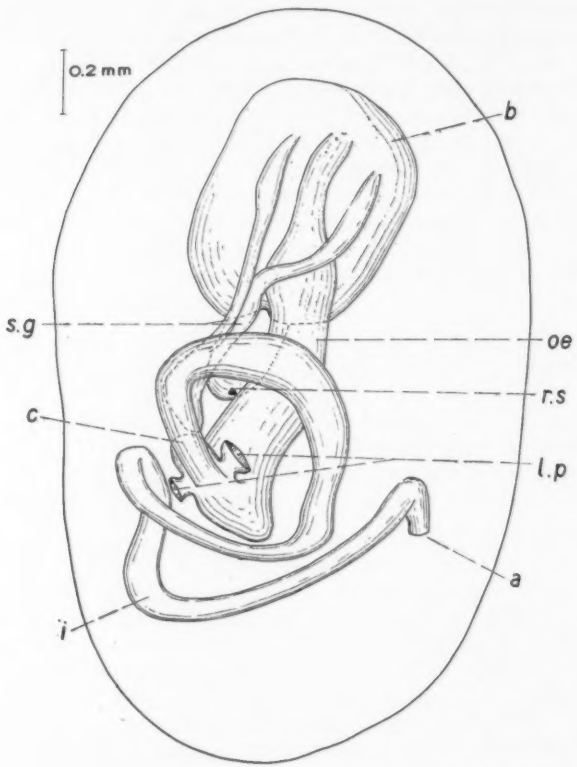

Fig. 16.—*Acroloxus improvisus.* Diagram of alimentary system with liver removed, in dorsal view. *a*, anus ; *b*, buccal bulb ; *c*, coecum ; *i*, intestine ; *l.p*, liver pores ; *oe*, oesophagus ; *r.s*, radula sack ; *s.g*, salivary glands.

strong and long cilia. There is no sac-like main part in the kidney. The whole system, kidney and urethra, forms a long serpentine duct which is located in the mantle border of the right side of the animal. Slightly less than half the serpentine duct is excretory whereas more than its distal half forms the urethra proper. The extremely narrow renal pore is located on the inside or under side of the mantle border.

Alimentary system. The buccal bulb is proportionately large (Fig. 16) but has a very weak jaw of a chitinised cuticula with a comparatively small number of thicker scales. The salivary glands, which pass through the nerve ring, are fused behind.

The radula (Fig. 17) has about 21 teeth in each row. The centrals are symmetrically bicuspid but the epithem seems to be more extended on the right cusp than on the left one. The four laterals on either side are unicuspid. The marginals consist only of a thin base and cusps are there completely lacking.

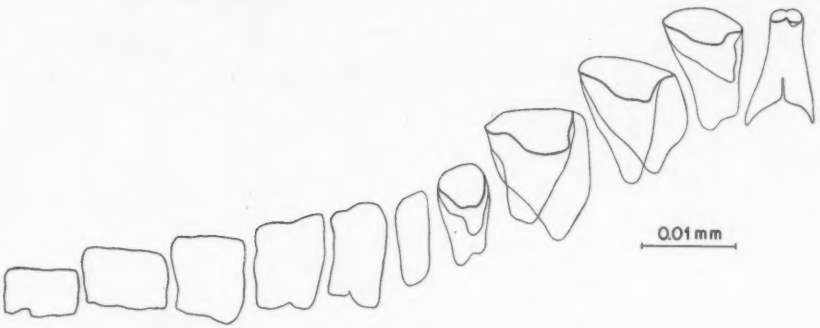

Fig. 17.—*Acroloxus improvisus.* Diagram of half a cross row from the radula in dorsal view.

The oesophagus widens abruptly in the region of the nerve ring. More posteriorly it widens gradually and merges into the stomach. The two liver pores are situated where the short caecum joins the junction between the stomach and the intestine. The latter has two loops. There is no trace of a gizzard, the whole alimentary tract behind the buccal bulb being thin-walled. Dorsally a large part of the visceral mass is occupied by the digestive gland.

Central nervous system. In addition to the cerebral, pedal and buccal ganglia there are only three more ganglia, all belonging to the visceral commissure. The two anterior ones, one to the left and one to the right, contain pleural and parietal ganglionic elements. The third is the abdominal ganglion.

Reproductive system (Fig. 18). The hermophrodite duct leads from the apically situated and comparatively compact gonad. The hermaphrodite duct has a vesicula seminalis, about half way between its junctions with the gonad and the uterine gland complex. The vesicula is an irregularly shaped, thin-walled, inside ciliated bladder-like formation.

The hermaphrodite duct joins the duct from the albumen gland and a small blind sac before it arrives at the uterine gland complex proper (Fig. 19). The common duct does not branch into a male and female duct before it joins the uterine gland complex. The only connexion between this duct and the prostate

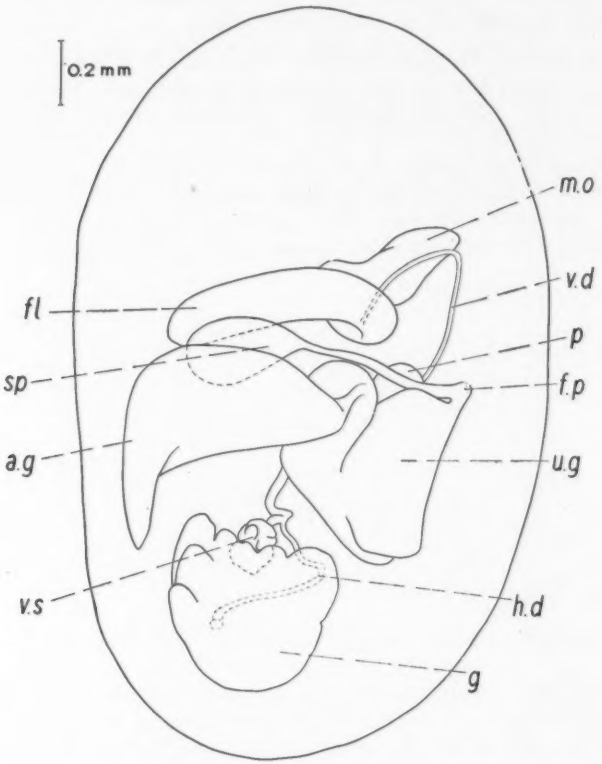

Fig. 18.—*Acroloxus improvisus*. Diagram of the reproductive system in dorsal view. *a.g*, albumen gland ; *fl*, flagellum ; *f.p*, female genital pore ; *g*, gonad ; *h.d*, hermaphrodite duct ; *m.o*, male copulatory organ ; *p*, prostate ; *sp*, spermatheca ; *u.g*, uterine gland complex ; *v.d*, vas deferens ; *v.s*, vesicula seminalis.

is through part of the uterine gland complex. The latter has thick glandular walls and three large internal folds of glandular epithelium. The spermatheca is more or less pear-shaped and connected with the uterine complex at the female pore through a slender duct.

The prostate is roundish and contains a single layer of tall glandular cells. The vas deferens goes out from the prostate and enters the male copulatory organ, after a loop through the subdermal tissue (Figs. 20 and 21). The latter has a preputium which is considerably shorter than the penis sheath. The

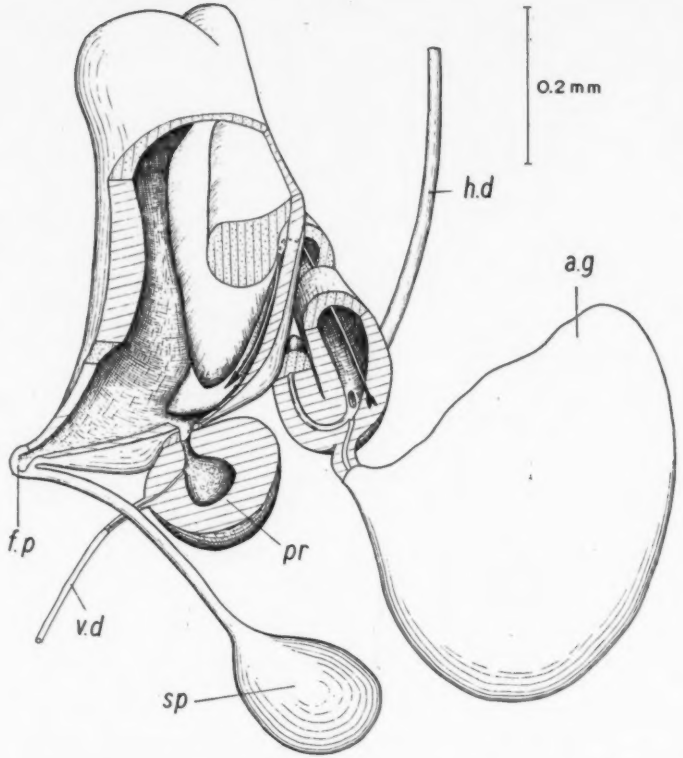

Fig. 19.—*Acroloxus improvisus*. Stereogram of the uterine gland complex and adjacent structures in oblique dorso-anterior view ; the arrow indicates the course of the lowest part of the common duct.
a.g, albumen gland ; *f.p*, female genital pore ; *h.d*, hermaphrodite duct ; *pr*, prostate ; *sp*, spermatheca ; *v.d*, vas deferens.

lumen of the sheath is directly connected with that of the flagellum without any distinct narrowing. The flagellum is glandular. The penis hangs out from one side of the wall where it connects the penis sheath with the flagellum. The vas deferens open out laterally on the penis.

ACROLOXUS MACEDONICUS Hadžišče 1959

Acroloxus macedonicus is restricted to certain stretches of the shore zone in Lake Ochrid. It lives on limestone rocks and boulders, mostly on their under sides at a depth of about 30–50 cm. Material was collected from two different places with similar environments. About 150 specimens were collected below the old church on the point west of the town of Ochrid. This sample is called population II below. About 175 specimens were collected at a rocky part

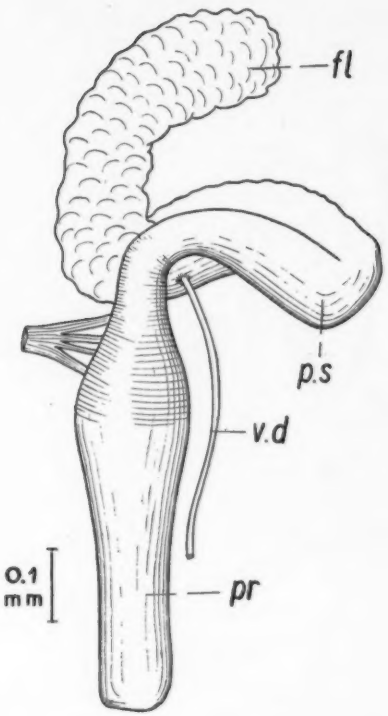

Fig. 20.—*Acroloxus improvisus*. Male copulatory organ.
fl, flagellum ; *pr*, preputium ; *p.s*, penis sheath ; *v.d*, vas deferens.

of the eastern shore about half way between Ochrid and the southern end of the lake. This sample is called population I below.

No specimens with mature gonad or with fully developed copulatory organs were found in the material obtained of this species. A probable explanation of this could be the occurrence of two generations per season. Among freshwater snails in general, the hibernating generation oviposits as soon as the hibernation period is finished. In Lake Ochrid this should occur in early spring. This generation then may die off whereas its progeny may become mature during middle or late summer, produce a new generation and die. This third generation may hibernate and reproduce the following spring. Such a life cycle seems probable for all the sexually immature material gathered by the author was collected in late August and early September (efforts to get material from other seasons have not been successful). Hunter (1953) has shown that in a Scottish environment *Ancylus fluviatilis* Müller dies soon after spawning and he also concluded the same probably occurs in *Acroloxus lacustris* (L.). Similar results have been obtained by Geldiay (1956).

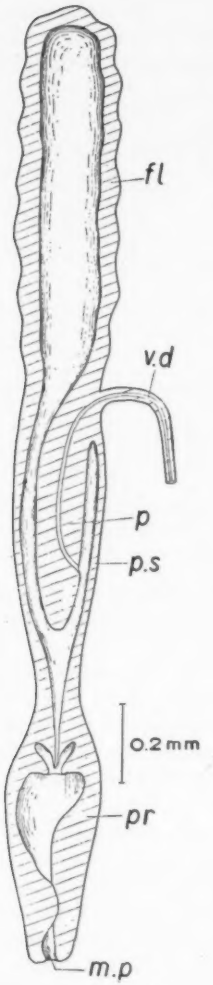

Fig. 21.—*Acroloxus improvisus*. Longitudinally-sectioned male copulatory organ. *fl*, flagellum ; *m.p*, male genital pore ; *p*, penis ; *pr*, preputium ; *p.s*, penis sheath ; *v.d*, vas deferens.

The shell. The form of the shell differs between population I and II, therefore the shell structure of each population is described separately.

Population I (Pl. 4, Figs. 2–4). In the available material the shell length does not reach three millimetres. The length/breadth ratio is 1·37 among the larger specimens, in the smaller ones slightly less (cf. Fig. 22). This means that in young specimens the shell is proportionately somewhat broader than in

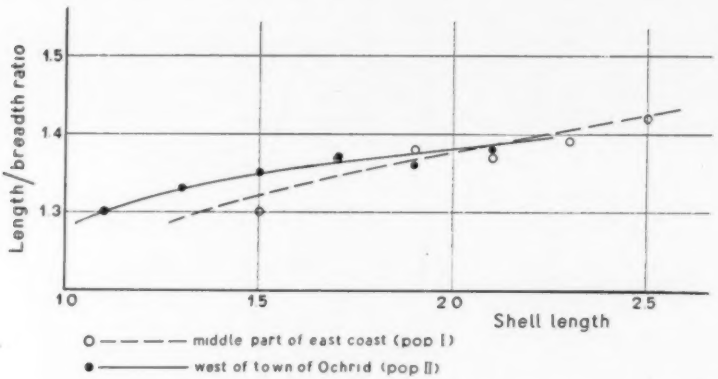

Fig. 22.—*Acroloxus macedonicus.* Diagram showing the relationship between length/breadth ratio of the shell and the shell-size in the two populations examined. Points indicate means of ratio within the respective size group.

adults. The shell height varies from more than one-fourth of the shell length in young specimens to less than one-fifth of the shell length in the adult or almost adult specimens.

The form of the aperture, i.e. the circumference of the shell, varies considerably. It is normally obliquely elliptic. The anterior end of the shell is often located to the left and its posterior end to the right of the median line. The apex, which points posteriorly and slightly to the left, is located to the left of the median line and about one-fifth of the shell length or less from the posterior margin of the shell.

There is generally a concavity in the shell surface behind and laterally to the apical region. Anterior to this region, there is often a slight convexity but in older shells sometimes a concavity (cf. Pl. 4, fig. 6). More peripherad, anteriorly and laterally but not posteriorly, the shell surface is more or less convex.

The apical region has a fine sculpture of radiating ridges, normally 30 to 35 in number (Pl. 4, fig. 3). Between these radial or longitudinal ridges there are, at least on the lower part of the peripheral region, extremely fine transverse ridges. Often there are at least peripherally, secondary ridges between the main longitudinal ridges. More peripherally, below the apical region an extremely tiny radiating microsculpture can occur. Concentric growth lines can be present to a varying degree. Much more pronounced, and easily detectable, is the stronger sculpture covering the whole shell below the apical region. This sculpture consists of rounded ridges, giving the whole surface a wavy

appearance; Their degree of development varies considerably. Sometimes only 5 to 15 large ridges, which protrude at the shell margin, are present. In roughly 30 per cent of the shells, they are more numerous but smaller, and only slightly affect the form of the shell margin. However, the radiating macrosculpture is always present. The strongest ridges are those directed anteriorly.

Population II (Pl. 4, figs. 5 and 6). The length/breadth ratio of the shell in the material at hand shows a very slight difference from that in population I (Fig. 22) but the difference cannot be proved to be significant.

The radial macrosculpture is missing or almost missing. A slight indication of a macrosculpture occurs in about 20 per cent of the shells. This

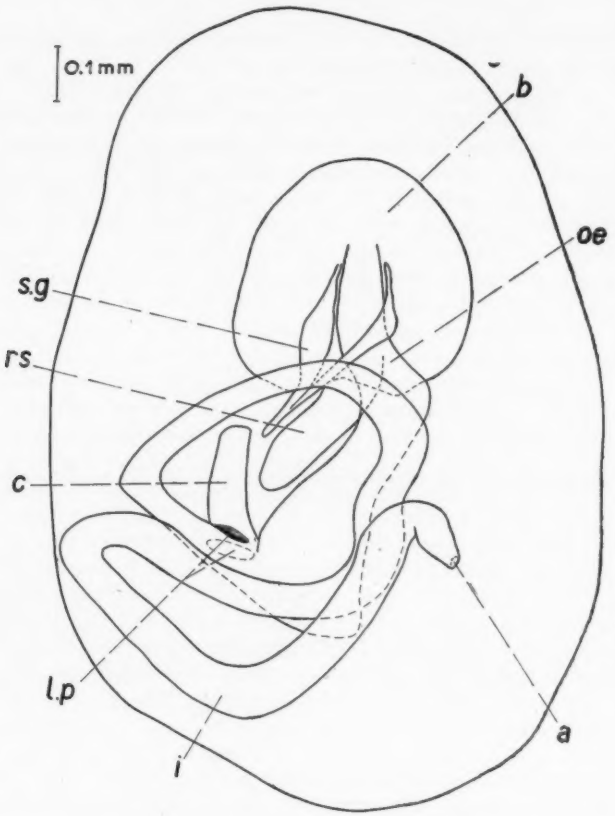

Fig. 23.—*Acroloxus macedonicus*. (Population I). Diagram of alimentary system with liver removed, in dorsal view.

a, anus; *b*, buccal bulb; *c*, cecum; *i*, intestine; *l.p*, liver pores; *oe*, oesophagus; *rs*, radula sack; *s.g*, salivary gland.

structure is much weaker than in population I and never affects the form of the shell margin. In population II the ridges, even when present, can only be detected with difficulty when a light beam is directed at a certain angle on the shell.

Apart from the differences mentioned above, the two populations are characterised by the same shell features.

The animal. Inside the mantle border the dorsal side of the body is pigmented with a cellular pattern. Above the shell adductors pigmentation is absent. The external shape of the animal is similar to that in *Acr. improvisus*, though some proportions are different. The pseudobranch is longer in *Acr. macedonicus*, reaching down almost to the level of the sole of the foot.

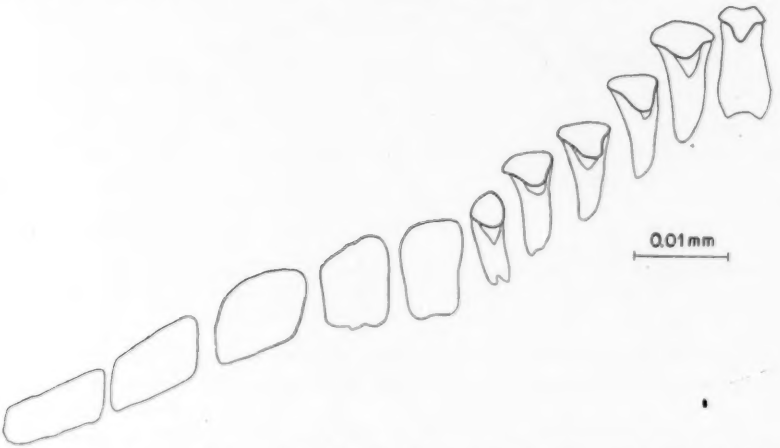

Fig. 24.—*Acroloxus macedonicus*. Population I. Diagram of half a cross row from the radula in dorsal view.

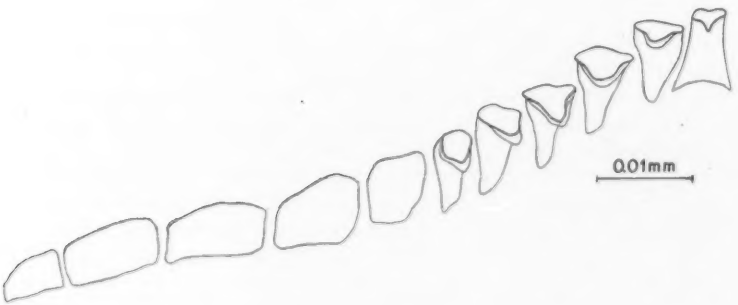

Fig. 25.—*Acroloxus macedonicus*. Population II. Diagram of half a cross row from the radula in dorsal view.

The general internal organisation, the pallial organs and the alimentary system are mainly similar to corresponding features in *Acr. improvisus*. The caecum from the junction between the pylorus region of the stomach, and the intestine, is proportionately longer and slenderer in *Acr. mazedonicus* (Fig. 23). The central teeth of the radula are unicuspid, like the lateral ones. The marginal teeth consists of a base only and lack any trace of cusps. There is no significant difference between the radula in population I (Fig. 24) and population II (Fig. 25).

It has not been possible to examine the reproductive system because the specimens were not mature (see p. 520 above).

DISCUSSION

Apart from the endemic species in Lake Ochrid and in Lake Baikal, and a probably distinct form on the island of Madeira, there are only two species of Ancylidae in the Palearctic region. Both have a wide distribution. *Ancylus fluviatilis* Müller is spread over most of Europe, northwest Africa, and Caucasia. *Acroloxus lacustris* (L.) is spread over most of Europe, northern Asia and Caucasia. Both species occur in Lake Ochrid or in close connexion to it. *A. fluviatilis* is present near the southern end of the lake in a spring, which forms one of the main tributaries to the lake. Two specimens of *Acr. lacustris* were found at the shore of the lake at the town of Ochrid.

The anatomy of the endemic *Ancylus* and *Acroloxus* species of Lake Ochrid shows that these species are closely related to *Ancylus fluviatilis* and *Acroloxus lacustris* respectively. The anatomical similarities are such that it is reasonable to assume an origin of the endemic Ochrid species from *Ancylus fluviatilis* and *Acroloxus lacustris*. The origin of the endemic Ochrid Ancylidae and the two mentioned species from near, common ancestors is also a possibility. The peculiar shell characteristics of the endemic Ancylidae of Lake Ochrid have never been recorded in any fossil ancylids.

Anatomical examination also shows that the endemic species of *Ancylus* in Lake Ochrid are closely related. *A. tapirulus* and *A. scalariformis* have no essential differences other than shell characteristics. The same is true for *A. scalariformis* and *A. lapicidus* though these two species are both characterized by the same peculiar type of shell. These two species have apparently separated by speciation from a common ancestor, which has earlier evolved from the ordinary ancylid type (as shown by *A. tapirulus* and *A. fluviatilis*)

It has not been possible to examine *Acroloxus macedonicus* thoroughly but all observations made so far indicate a close relationship between this species and *Acr. improvisus*. The radula has greater similarity in these two species than between them and *Acr. lacustris*.

The endemic Ancylidae of Lake Ochrid have never been recorded from outside the lake as living snails or as fossils. This fact, together with the general occurrence of Ancylidae in the Palearctic region, makes it *a priori* reasonable to suspect that the endemic species of Lake Ochrid have evolved through intralacustrine speciation. Their distribution within the lake provides some support for this supposition.

Lake Ochrid has a simple form with a comparatively even slope down to the maximum depth of 286 metres. The shore consists of rocks, boulders, gravel, or sand, rarely mud. Below that follows a number of concentric depth-zones providing different environments for the animal life. Immediately below the shore there is often a zone with vegetation consisting of *Phragmites*, *Potamogeton*, and other plants. Between about 7 and 18 metres the bottom is occupied by *Chara* meadows, and deeper, between about 18 and 35 metres, follows the shell zone. In that zone living specimens and empty shells of the bivalve *Dreissena polymorpha* (Pallas) dominate in the bottom material. Below the shell zone follows the profundal zone.

The ancylid species of Lake Ochrid do not occur in the *Chara* zone and the profundal zone, but are restricted to the shore zone and the shell zone. *Ancylus tapirulus* and *A. scalariformis* as well as *Acroloxus improvisus* live exclusively in the latter, whereas *Ancylus lapicidus* and *Acroloxus mazedonicus* are restricted to the shore zone. *Ancylus scalariformis* and *A. lapicidus* are, as mentioned above, apparently closely related and form a pair of species with one living in each of the two depth zones separated by the *Chara zone* devoid of ancylids. *Acroloxus improvisus* and *Acr. macedonicus* form a similar pair. If the non-endemic species are included in the discussion *Acr. lacustris* and *A. improvisus* can likewise be regarded as a similar (but not so closely related) pair of species. The same is true for *Ancylus fluviatilis* and *A. tapirulus*. The two species of one pair might have undergone a certain independent evolution in their separate habitats while the intermediate *Chara* zone has acted as an isolating agent.

The efficiency of such an isolating agent is emphasized by the extremely patchy distribution of the ancylid populations in the shell zone. During dredging several hauls can be done in apparently the same spot, with the same bearings to the same landmarks, and ancylids may be obtained in one of the hauls only. In that single haul, however, 50 to 100 specimens may be obtained. This patchy distribution of the populations indicates a low mobility of the individuals. The presumably low number of eggs (according to studies on *Ancylus fluviatilis* by Bondesen, 1950, and Hunter, 1953) may also to some extent contribute to the isolated conditions of the populations. A larger number of eggs would statistically increase the chance of random dispersal, active or passive.

The distribution of the species pairs in the lake only gives indirect evidence of intralacustrine speciation. As far as the origin of the species involved is concerned intralacustrine speciation, though probable, is still hypothetical. The case of intraspecific differentiation in *Acr. mazedonicus*, however, presents direct evidence of intralacustrine evolution in progress.

Acr. macedonicus is confined to a certain type of shore habitat, i.e., limestone boulders a few decimetres below the water surface. Such habitats are present along certain parts of the shore and separated by stretches where the environment is unsuitable for the species. For this reason the stock of *Acr. macedonicus* in Lake Ochrid is divided up into isolated populations. Two such populations have been described above under the designation I and II. Further

populations may be present, *e.g.*, on the limestone parts of the Albanian coast, which has never been properly explored.

The two populations studied are morphologically different and must be regarded as two geographical races of one species. The difference in shell sculpture cannot be ecophenotypical or due to influence from different environmental conditions. The environments where the two populations live are similar. The only possible influence by the environment on the shell sculpture should be related to the water movement. The small size of the shells, the small-scale difference in shell sculpture, and the inertia of the water makes it practically impossible to assume a specific ecophenotypical influence on the shell sculpture in each habitat. It is not reasonable to assume anything but a genetical background to the difference in shell sculpture between the two populations. This is evidence for a certain amount of independent evolution in the two populations, or at least in one of them. This, finally, is evidence for the presence of an efficient intralacustrine geographical or micro-geographical isolation.

The vertical and horizontal intralacustrine micro-geographical isolations described above are ecologically based. This does not mean that the populations were primarily ecologically isolated, or that their independent evolution from a common ancestor was originally due to ecological separation. It implies that the geographical distribution in the lake of certain environmental conditions favours a certain micro-geographical pattern of distribution within the lake of the populations belonging to one species. This involves isolation of populations or groups of populations from each other and, therefore, this pattern of distribution favours speciation.

The term " geographical isolation " is well established in the literature on organic evolution. In connexion with intralacustrine speciation the literal meaning of the term is not adequate because the dimension commonly implied in the word " geographical ". The true dimension of the isolation is better expressed by the term " micro-geographical ". But neither geographical nor micro-geographical emphasizes the essential point of the concept. The dimension in space of the isolation is of secondary importance. The dimension necessary depends on the motility and faculty of passive dispersal of the animals concerned as well as on local conditions. The essential point is that there is an effective reproductive isolation by means of space. Therefore " spatial isolation " would be a more adequate term than geographical isolation. As far as intralacustrine speciation is concerned the term spatial isolation is particularly to be recommended because it is apparent that the term geographical isolation tends to support a preconceived opinion about the possibility of intralacustrine speciation.

Not only in limnic but also in other environments the term geographical isolation may be less adequate than spatial isolation. This will be exemplified here by one case only. Staiger (1954) has found in Brittany that the marine littoral snail *Nucella lapillus* (L.) has a different chromosome constitution in populations in different types of environment. One type of chromosome set is found in populations on rocks subject to strong wave action, another type in sheltered populations among brown algae. The food supply differs between

the two environments. Populations in intermediate environments are heterogenous with regard to the chromosome constitution. These conditions, observed on the chromosome morphology but reasonably due to genotypical preferences to certain environmental conditions, must have evolved under spatial isolation (*Nucella* does not have a free-swimming larval stage). This spatial isolation is, however, of much smaller scale than expressed by the term geographical isolation.

SUMMARY

The endemic Ancylidae of Lake Ochrid (three species of *Ancylus* and two species of *Acroloxus*), have been described conchologically and anatomically. One of the species, *Ancylus lapicidus*, is new. Another of the species, *Acroloxus macedonicus*, occurs in separated populations with different morphological characteristics. These characteristics are concluded to be genotypical. Two species are confined to the shore zone, three to the shell zone. These two depth zones are separated by the intermediary *Chara* zone. The occurrence of the ancylid populations is spotted.

The distribution of the ancylid species in Lake Ochrid is discussed ; the spotted distribution of their populations, and the occurrence of Ancylidae in the Palearctic region in general leads to the conclusion that intralacustrine speciation is probable among Ancylidae in Lake Ochrid.

It is pointed out that the term " spatial isolation " is much to be preferred to " geographical isolation " in confined areas and therefore would have a more universal applicability.

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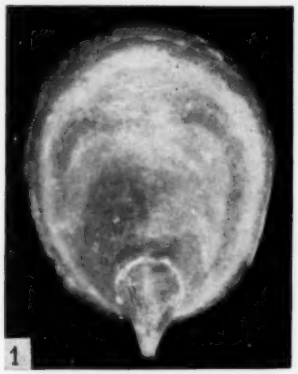
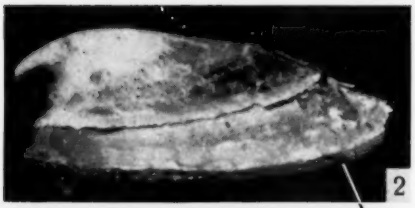
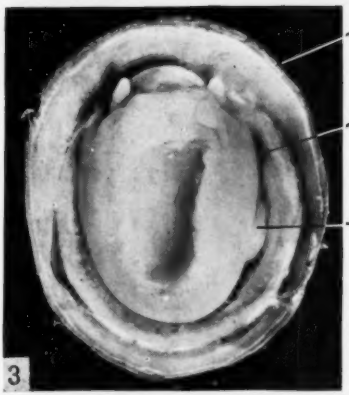
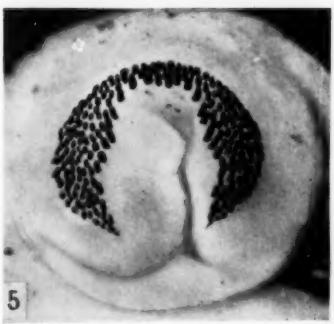


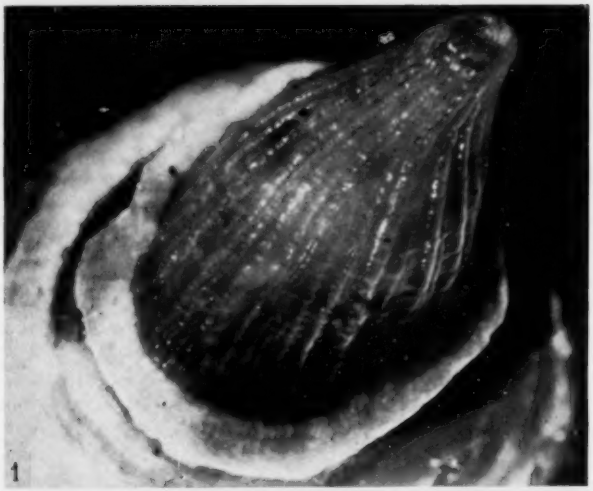




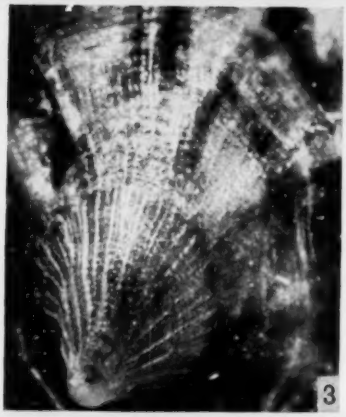


1–5.—*Ancylus tapirulus* Polinski. 6.—*Ancylus scalariformis* Stanković and Radoman.

1–3.—*Ancylus scalariformis* Stanković and Radoman.
4–6.—*Ancylus lapicidus* sp. n.



1–3.—*Ancylus lapicidus* sp. n.
4–5.—*Acroloxus improvisus* Polinski.



1.—*Acroloxus improvisus* Polinski.
2–6.—*Acroloxus macedonicus* Hadžišče.

EXPLANATION OF THE PLATES

Plate 1

Figs. 1—5.—*Ancylus tapirulus* Polinski. 1. Dorsal view, 13 ×. 2. Right side view, 15 ×. 3. Ventral view, 13 ×. 4. Dorsal view of apical region, 42 ×. 5. Ventral view of the mouth with the expanded jaw, 54 ×. Fig. 6. *Ancylus scalariformis* Stanković & Radoman. Ventral view, 17 ×. e.p., eaves-like projection; l, lateral flap or pseudobranch; m, mantle border; p, periostracum.

Plate 2

Figs. 1–3.—*Ancylus scalariformis* Stanković & Radoman. 1. Dorsal view, 13·5 ×. 2. Right side view, 13·5 ×. 3. Dorsal view of another specimen, 13·5 ×. Figs. 4–6. *Ancylus lapicidus* sp. n. 4. Dorsal view, 22 ×. 5. Left side view, 22 ×. 6. Ventral view, 25 ×.

Plate 3

Figs. 1–3.—*Ancylus lapicidus* sp. n. 1. Oblique dorsal view of apical region, 57 ×. 2. Dorsal view of young specimen, 31 × 3. Right side view of young specimen, 31 ×. Figs. 4–5. *Acroloxus improvisus* Polinski. 4. Oblique right side view, 22 ×. 5. Dorsal view, 20 ×.

Plate 4

Fig. 1.—*Acroloxus improvisus* Polinski. Ventro-lateral view of the left side, 22 ×. Figs. 2.–4.—*Acroloxus macedonicus* Hadžišče from the middle part of the east coast of Lake Ochrid (Population I). 2. Dorsal view, 32 ×. 3. Dorsal view of the apical region, 57 ×. 4. Right side view, 32 ×. Figs. 5–6.—*Acroloxus macedonicus* Hadžišče from the northern part of the east coast of Lake Ochrid (Population II). 5. Dorsal view, 34 ×. 6. Left side view, 44 ×. (Pls. 1-4, D. Berg photo.).

STUDIES ON THE FUNCTIONAL MORPHOLOGY OF *GERRIS NAJAS* DEGEER (HEM. HET. GERRIDAE)

BY

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(With 9 figures in the text)

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INTRODUCTION

There have been many studies of particular aspects of heteropteran morphology, but comparatively few detailed accounts of individual species.

In the following account only those aspects of the morphology of *Gerris najas* Deg. which are of functional significance or new interpretations will be considered, a full account is presented elsewhere (Brinkhurst, 1958). Several experiments were carried out to determine the function of various systems, and these will be described with the relevant morphology.

METHODS

Morphology

The morphology of *Gerris najas* was investigated by dissection and serial sections of both adults and nymphs. Serial sections were prepared from material fixed in alcoholic Bouin, and stored in 70 per cent alcohol. A triple-embedding technique using celloidin was found to be most satisfactory;

cedar-wood oil was used for clearing. Sectioning was attempted without the use of softening agents so as to prevent distortion, but this was not altogether satisfactory as the cuticle was rendered brittle by the use of heat and alcohol and frequently shattered under the knife. Sections were cut at 10 μ.

Most of the necessary observations were made by dissection of these relatively large insects ; only the details of the mouth parts and the genitalia required minute microscopical examination. Male and female genitalia were everted by submerging the insects in boiling water and applying gentle pressure to the abdomen. Genitalia were also examined *in situ* in living insects.

Dissections of a number of *Gerris* species were made and it was concluded that *G. najas*, apart from the male genitalia and the absence of wing muscles, is typical of the genus.

Experimental Work

Surface tension was measured by finding the weight required to pull a platinum ring of 13 mm. diameter through the surface film from below. The ring was suspended from the arm of a torsion balance, and the weight was recorded in milligrams after the balance had been adjusted to zero with the ring attached. Then $\frac{\text{weight in milligrams} \times \text{G}}{\text{circumference of the ring} \times 2} = \text{surface tension in dynes/cm.}$ Here G = 981 cms./sec^2, circumference = 13 mm. $\times$ 3·142 and therefore by substitution, surface tension = weight $\times$ 0·123.

Experiments were carried out to ascertain the lowest value of the surface tension at which various species could maintain themselves upon the film, this being termed the limiting value. Five individuals of one species were used for each observation. These were placed on a shallow dish in which was a thin film of water (surface tension = 70·8 dynes/cm.). The surface tension was lowered by the addition of a 0·5 per cent by volume solution of Teepol, a commercial detergent. This was applied drop by drop from a burette. The surface tension was measured prior to the addition of Teepol as a control, and after at least three individuals had sunk through the surface film. The ring was heated to red heat after each observation and three such observations were made on each species. In the case of *G. najas* one observation was made using a 0·5 per cent by weight solution of sodium tauroglycocholeate (bile salt) to see if the detergent by itself had any harmful effect. The limiting values obtained were : Teepol 42·2, 43·5, Bile salt 44·9. These figures indicate in general terms that there is no very marked effect due to the use of detergents as opposed to other, non-detergent, surface active substances.

Attempts were made to use a Du-Nuoy tensiometer in the field but it proved impossible to measure the strength of the actual film on the water (as opposed to that of a sample) with any certainty because the ring was disturbed by even the slightest water movement. The few values obtained were all very close to that of pure water, and after laboratory experiments had shown that the limiting values lay below the figures for surface tension obtained by Goldacre (1949) in the field the attempt was abandoned.

The direct measurement of rowing ability

Fig. 1 shows the apparatus used in comparing the rowing ability of two polymorphic forms of the same species. A single nylon strand separated from a length of nylon thread was fixed to the insect by means of a drop of sealing wax. The insect was then placed on a large shallow dish containing

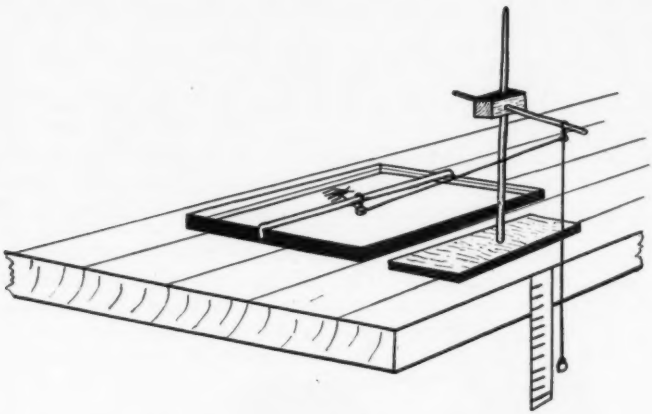

Fig. 1.—Sketch of the apparatus used to measure rowing ability.

water. A glass rod was supported above the water, in the centre of which was a platinum ring. By the side of the tank and at a height of about one foot above it was a second rod, held in place by a burette stand, with a similar platinum ring on the end of it. The thread from the insect was passed through the lower loop and then the upper loop, from which it hung past a scale fixed to the edge of the bench. The free end of the thread was then weighted with pieces of five amp. fuse wire such that an inactive gerrid would be pulled over the surface until it was directly beneath the lower ring. As soon as it attempted to row the weight would diminish the distance travelled, due to the extra load, to just that extent which provided a suitable range of movement, measured by the rise and fall of the weight past the centimetre scale. This weight was determined by many trials, and it was found that *G. lacustris* gave the best result when pulling three milligrams, which was then used in all subsequent experiments with this species.

The lower ring was fixed in the centre of the tank so that whichever way the insect swam, the resulting pull on the thread was the same.

Ten individuals of each polymorphic form were used, each one being observed for the first twenty attempts to row and then discarded. Results were recorded to the nearest half centimetre (above 2 cms.) to which the weight was lifted.

Rowing mechanism

Following the experiments on rowing ability it seemed that more knowledge of the precise movements involved was required. A 16 mm. film was exposed at 64 frames/sec. in an electrically driven camera, which stood vertically above a small dish containing the insect. The dish had a centimetre scale marked on it for location of the insect on each frame of the film, and the camera was operated only as the insect swam over this scale. The resulting film was projected at 16 frames/sec. and subsequently a series of individual frames were drawn.

THE HEAD

The structure of the head in Heteroptera is in general well understood but several points have received scant attention. The confused terminology of the external sclerites has been discussed by Southwood (1953) in whose paper the hypopharynx is clearly identified. This structure is complex in Heteroptera and is known to carry the cibarial and salivary channels between the maxillae,

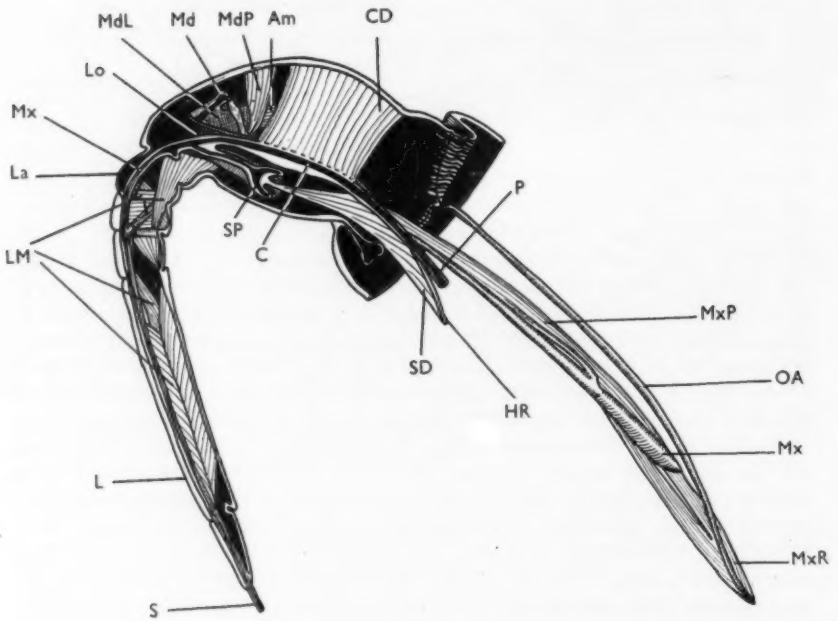

Fig. 2.—Diagramatic sagittal section of the head (re-drawn after Weber).
Am., antennal muscle; C., cibarium ; CD., cibarial dilators ; HR., hypopharyngeal rods ; L., labium ; La., labrum ; LM., labial muscles ; Lo., lorum ; Md., mandible ; MdL., mandibular lever ; MdP., mandibular protractor ; Mx., maxilla ; MxP., maxillary protractor ; MxR., maxillary retractor ; OA., occipital apodeme ; P., pharynx ; S., stylets ; SD., salivary pump dilator ; SP., salivary pump.

although the nature of this junction has not been clearly described. The two maxillae are brought together at the point at which they emerge from the head and the two ducts formed by the close approximation of their grooved inner surfaces must clearly be continuous with the cibarial and salivary channels for the two pump mechanisms to operate.

The general morphology of the head is shown in Fig. 2 which is re-drawn after Weber (1930). From this it is clear that the cibarium opens anteriorly on to the top of the hypopharynx and is itself apparently roofed by the labrum (by the labrum-epipharynx as shown below) whilst its two sides are formed by the maxillae. It will be noticed that these are exactly the morphological relations of the mouth in mandibulate insects. The salivary channel can be seen running through the body of the hypopharynx but the remainder of this structure is not shown in the figure. Similarly the proximal and distal end of the maxilla may be seen on one side, but the middle part of the stylet and its position with regard to the hypopharynx are not shown. The proximal part of the maxilla is associated with a long apodeme which arises from the cervical area of the head, bearing the origin of the retractor muscle. The long protractor muscle runs the length of the stylet from the maxillary plate to its insertion on the forked proximal end of the shaft.

A more detailed picture of the structures in the head can only be built up from a series of transverse sections as illustrated in Fig. 3. The levels at which these sections were cut is illustrated in Fig. 3A. The stylets are shown distally within the labial groove in Fig. 3B, the larger of the two spaces between the maxillae being the food channel. Fig. 3C shows the labium, here roofed over by the long epipharynx, in the normal position with the stylet groove uppermost. The ephipharynx is developed from the ante-clypeus, not the labrum (Fig. 4A). Fig. 3D shows that, just at the point where the stylets enter the labial groove, the maxillae are bound together by a membrane, outside which lie the mandibles, both pairs of stylets being roofed by the ante-clypeus. In the next section (3E) the maxillae are no longer closely opposed but the forward-projecting lobe of the hypopharynx can be clearly seen. In the body of this lobe lies the salivary duct, and the top of the lobe forms the floor of the cibarium. The roof of the cibarium is formed by the inner wall of the ante-clypeus/frons and even as far forward as this the cibarial dilator muscles can be seen. The ante-clypeus is completely separated from the maxillary plate although both the latter and the hypopharynx fit closely against it and must maintain that position in life for the food meatus to be continuous. From this point forwards the hypopharynx narrows rapidly and is inserted between the maxillae as these are presented together before entering the membrane described above. The mandibles retain their lateral position and the stylet groove in the maxillary plate becomes continuous with that of the labium.

It remains to be seen how the food channel connects with the cibarial pump. As illustrated in Fig. 2 the roof of this pump is formed by the inner wall of the ante-clypeus/frons throughout. In mandibulate insects the mouth opens above the hypopharynx where this projects from the head as a median lobe and, in *Gerris*, the mouth is simply withdrawn on the end of a

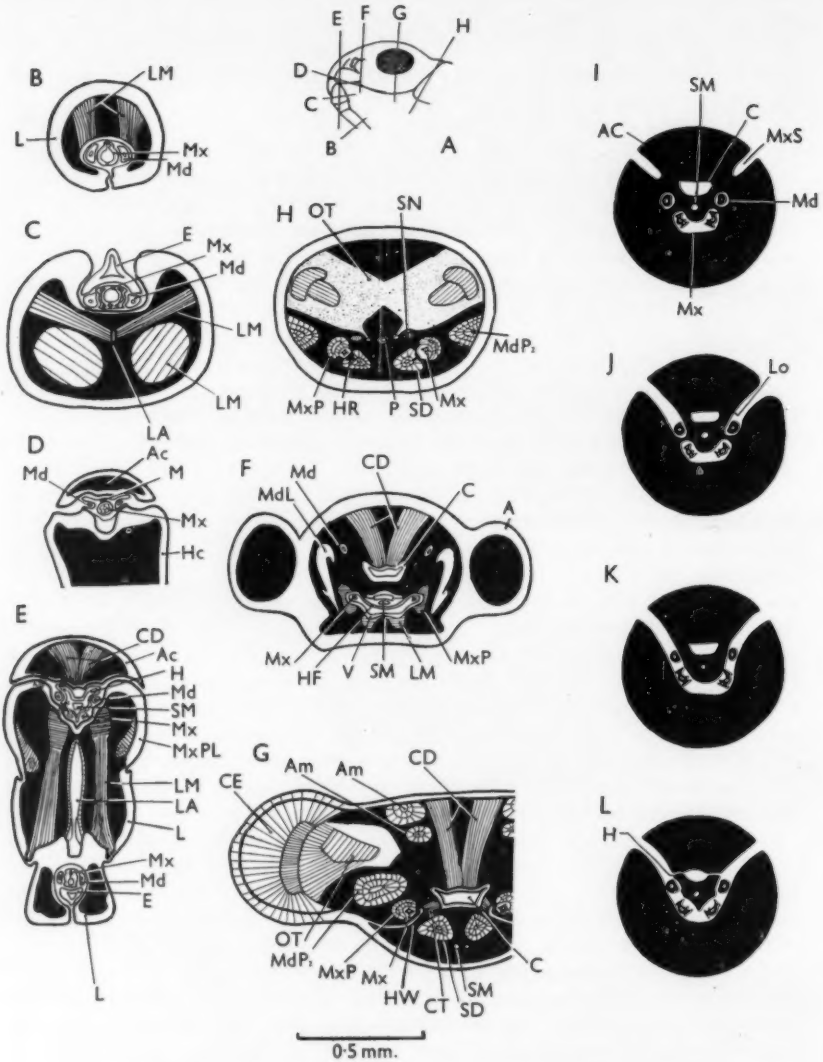

Fig. 3.—A, sketch to show levels at which sections of the head were made. B–H., transverse sections of the head ; I–L., theoretical sections. A., antennal base ; AC., ante-clypeus ; Am., antennal muscle ; C., cibarium ; CD., cibarial dilators ; CE., compound eye ; CT., cibarial tensor ; E., epipharynx ; H., hypopharynx ; HC., head capsule ; HF., hypopharynx floor ; HR., hypopharyngeal rod ; HW., hypopharyngeal wing ; L., labium ; LA., labial apodeme ; LM., labial muscle ; Lo., lorum ; M., membrane linking maxillae ; Md., mandible ; MdL., mandibular lever ; MdP., mandibular protractor ; Mx., maxilla ; MxPL., maxillary plate ; MxP., maxillary protractor ; MxS., maxillary suture ; OT., optic tract ; P., pharynx ; SD., salivary pump dilators ; SM., salivary meatus ; SN., stylet nerve ; V., ventral plate.

long pre-oral tube which opens on to the hypopharynx in the original oral position. In order to understand fully how the structure shown in Fig. 3E becomes that of 3F the maxillary suture must be considered in detail. This suture separates both the jugum and maxillary plate in turn from the ante-clypeus on each side, starting as a shallow groove which gradually deepens anteriorly. As it does so, it fuses first with the mandibular stylet sacs and then with the confluent space of the maxillary stylet sacs, so the stylets are now morphologically extracranial. Davidson (1914) assumed that the inner walls of this suture constituted the plate subsequently termed the lorum by Southwood (1953). Just anterior to this point the cibarial cavity becomes confluent with that formed by the fusion of the maxillary sutures, the mandibular and the maxillary stylet sacs, and so separates off the median hypopharyngeal lobe from the ante-clypeus. The limits of the constituent parts of the complete space so formed are indicated on Fig. 3E by six parallel lines at A, B and C, and it can be seen that fusion of the walls at these three points on each side would convert Fig. 3E into Fig. 3F (ignoring the antennal bases in the latter). It is necessary to visualise the various plates of the head as merely the outer walls of complete lobes or divisions of the inner haemocoel, and to consider the fate of each particular space in order to appreciate these changes. The whole process of transferring the separate stylets and the food and salivary channels from the inside to the outside of the head is illustrated in a series of theoretical sections in Figs. 3I–3L. The essential details of all four sections have been identified at various times in serial sections of the head.

In section F the maxillae are seen to lie in a space presumably formed by the union of the two stylet sacs, but the walls have become variously sclerotised. The roof of the chamber is formed by the base of the hypopharynx, and its floor by the " ventral sclerite " (Guthrie, 1954). It seems possible that this latter is formed by an inversion of part of the maxillary plate, and it serves for the origin of the proximal labial muscles (Fig. 2).

Within the head the maxillae lie lateral to the hypopharynx, at first within the space described above. At the level of the salivary pump, however, the two halves of this space separate abruptly, their median ends turning down to meet the head capsule latero-ventrally, their original dorsal walls (the base of the hypopharynx) forming the hypopharyngeal wings. The original lower wall becomes indistinct but it is clear that each stylet lies in a space, the stylet sac, lateral to the wings (Fig. 3G). These wings serve to brace the majority of the important organs in the head against the head capsule. A series of short muscle fibres run between the cibarial floor and the inner ends of the hypopharyngeal wings on each side which serve to brace the cibarium against the latter. In the occiput the hypopharyngeal wings lose their connection with the floor of the head and become a pair of rods serving as the origin of the salivary pump dilator muscles (Figs. 2, 3H). An attempt has been made to show the hypopharynx in its entirety in Fig. 4B.

One further point remains to be discussed. Ekblom (1926) identified two muscles acting on the mandible and its lever, whilst Guthrie (1954) found three but retained the terminology employed by Ekblom, and thus the muscle

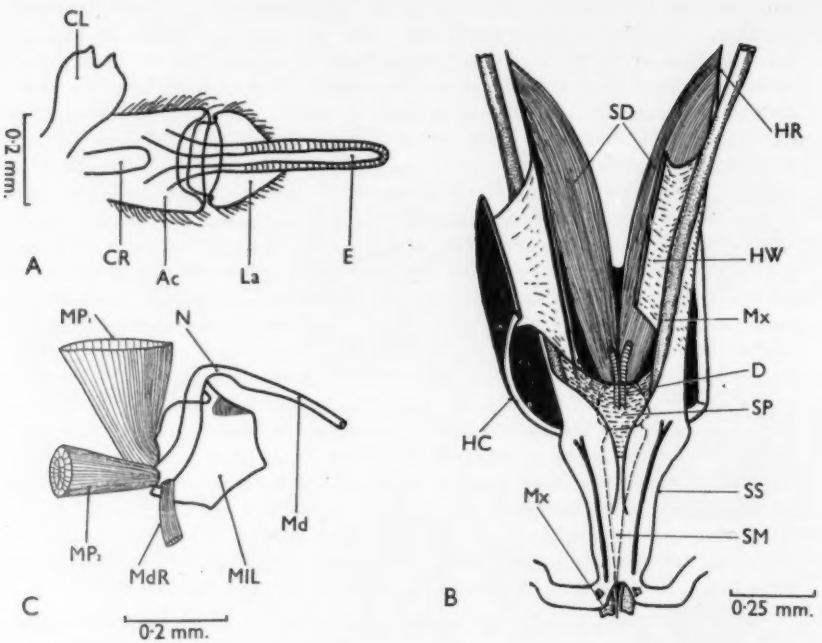

Fig. 4.—The head. A. The labrum and epipharynx ; B. The hypopharynx ; C. The mandibular plate and muscles.

AC., ante-clypeus ; CL., cibarial lip ; CR., cibarial roof ; D., salivary ducts ; E., epipharynx ; HC., head capsule ; HR., hypopharyngeal rod ; HW., hypopharyngeal wings ; La., labrum ; Md., mandible ; MdL., mandibular lever ; MdP., mandibular protractors ; MdR., mandibular retractor ; Mx., maxilla ; SD., salivary pump dilators ; SM., salivary meatus ; SP., salivary pump ; SS. stylet sac.

identified as protractor 1 in Fig. 4C was described as a retractor. The protractor of their accounts (termed protractor 2 in Fig. 4C) rotates the stylet about the lever where this is notched dorsally, the stylet bends at the neck just distal to this and so the shaft is protracted. It seems quite clear that the action of the dorsal muscle contributes towards this movement and should therefore be regarded as a protractor in addition. The only retractor would then be the small ventral muscle overlooked by Ekblom (1926). The reduction or absence of antagonistic muscles cannot be regarded as unusual, for in both the cibarial and salivary pumps antagonistic muscles are absent, their function being accomplished by the natural elasticity of chitin. It is clear that a considerable protractive thrust is developed over a short range of movement in the mandible, in contrast to the maxilla which moves through a considerable distance by the contraction of the long thin protractor. This is correlated with

the different functions of the stylets, the mandibles ensuring the initial penetration of the prey whilst the maxillae convey fluids in and out. Retraction of the stylets would no doubt be aided by the movement of the labium into the horizontal resting position after rejection of the prey.

THE THORAX

Introduction

In a paper on the evolution of water bugs, China (1955) outlined the major evolutionary trends towards life on the surface film of water. Three of these were :—the elongation of the pronotum, the movement of the tarsal claw from an apical to a pre-apical position, and the movement of the metasternal scent gland to a median ventral position.

A review of the functional morphology of *Gerris* throws some light on the significance of these and other changes. The thorax has been described previously by Larsen (1945) and Guthrie (1954) in general terms.

The external features

The prothorax is short (Fig. 5A) with the coxae inserted vertically, close together in the mid-line, and so restricting the sternal area. The epimeron and episternum are continued over the coxal base to form the supra-coxal flange as in other limbs. The pleura are continued posteriorly to overlap the mesonotum slightly, forming deep grooves in which are situated the prothoracic spiracles. Extending from this ridge dorsally the prothorax is continued as a protective lobe over the thin mesonotum and wing-bases, whilst anterodorsally the pronotum itself bears a pair of prominences associated with the origin of the tergo-coxal muscles.

The long mesothorax is formed of the fused sternal and pleural areas, with a thin mesonotum lying beneath the pronotal lobe. The mesonotum is membranous (Fig. 5B) in contrast to the heavily sclerotised ventro-lateral portion of this segment. The scutum bears anteriorly the prephragma, which curves ventrally to meet the incurved pleural areas. The lateral scutal areas are continued forwards as the post spiracular plates of the anterior spiracles and a small accessory sclerite lies ventral to each of these. Lateral to the scutum lie the prealary sclerites, the posterior ends of which bear the fore-wing bases. At this level a transverse suture delimits the scutellum from the scutum, and lying posterior to the scutellum is a distinct, crescentic post-scutellum.

The coxae are situated laterally and are horizontally inclined, and thus the epimeral-episternal suture is horizontal on the supra-coxal flange. The sternal area is correspondingly much broader than in the prothorax. Above the supra-coxal flange is the opening of the second thoracic spiracle on each side.

The metathorax is apparently short, the sternum being about one-third of the length of the mesothoracic sternum. The metatergum is U-shaped, extending forward as far as the fore-wing bases and bordering the scutellum and post-scutellum of the mesothorax (Fig. 5B), and so the internal volume of this segment is greater than might be supposed. The sternum bears a median lobe, on to which opens the scent gland. The epimera and episterna are fused

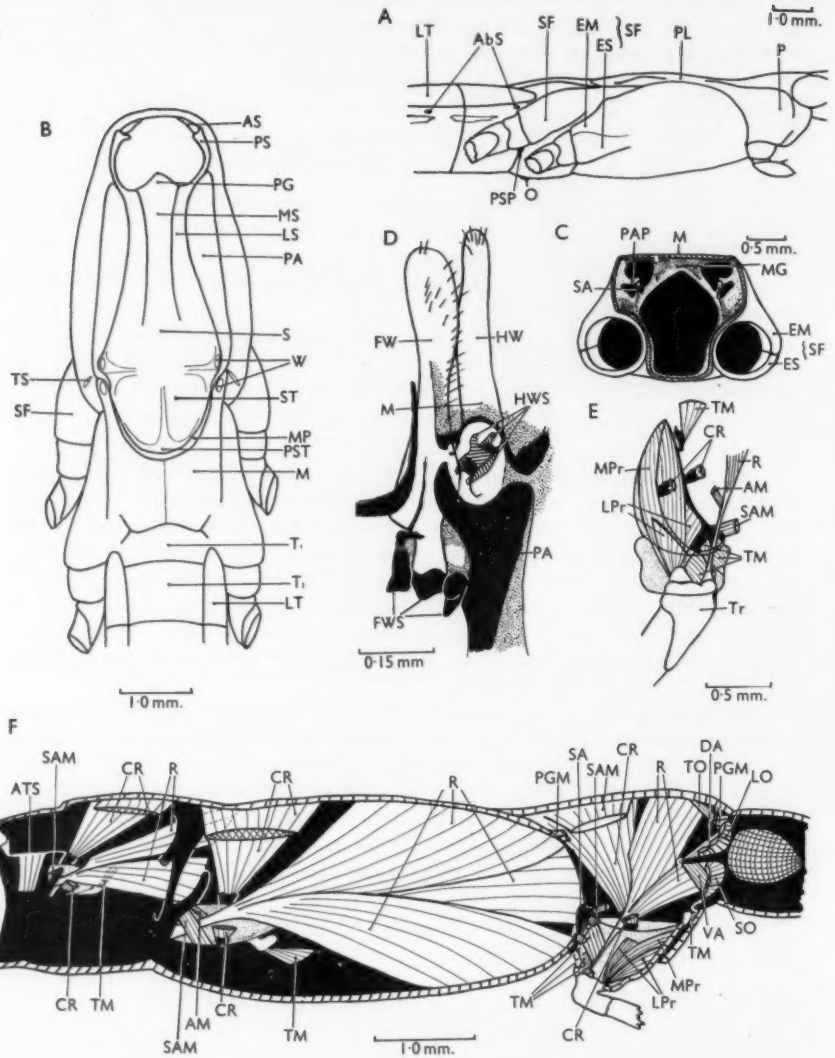

Fig. 5.—The thorax. A. External features, lateral aspect ; B. The mesonotum ; C. Transverse section of the mesothorax to show the apophyses ; D. The wings ; E. The muscles of the coxa ; F. Sagittal section of the thorax : muscles.

AbS., abdominal spiracles ; AM., accessory tendon muscle ; AS., accessory sclerite ; ATS., abdominal tergo-sternal muscle ; CR., coxal rotator muscles ; DA., dorsal apodeme

[*Continued bottom of next page*]

on the supra-coxal flange, whilst the coxae are similarly oriented to those of the mesothorax, lying slightly dorsal to them. The U-shaped tergum bears the hind-wing bases at its most anterior extremities, carrying these close to the fore-wings. The deep mesophragmal pit separates the post-scutellum from the metatergum in the mid-line.

A short prephragma arises from the median scutal area of the mesonotum, whilst the meso- and meta-phragmata are associated with the sternal and pleural apophyses. The sternal apophyses of the prothorax are short arms, bifurcate at the tips, which act as the origin of various muscles. The meso- and metathorax the sternal and pleural apophyses project inwards to unite, separating off the coxal cavities (Fig. 5C). The phragma is strongly developed in the mesothorax and bears a pair of dorso-lateral arms which join the pleural apophyses, forming a pair of dorso-lateral spaces which are part of the metathorax, roofed by the forward projections of the metatergum (see above). Thus the whole thorax is braced in this region to counteract the stresses set up in the mesothorax in rowing, and (in winged species) flight. The metathoracic apophyses are similarly developed but not to so great an extent. There are two trochantinal sclerites in each coxal base. The first lies at the proximal end of the coxa, the second of the coxal rim medially, or, in the metathorax laterally. The second sclerite bears a muscle in each case.

The thoracic appendages

The fore-limbs are raptorial and used in feeding, as in many other water-bugs. They are shorter than the other two pairs of limbs and differ from them in that they are inserted ventrally. These limbs are normally used as supports and do not participate in the rowing movements (see below). As in all three pairs of limbs, the claws lie at the base of a sub-apical notch, into which they can be withdrawn when on the water-surface. These claws are employed when the insect walks or climbs emergent vegetation.

The mid- and hind-limbs are long and are used in the normal mode of progression as well as in leaping, both off the water and also when on land. As the fulcrum of the limb is very close to its base, its elongation increases the leverage produced by the limb, and thus its rowing efficiency. Both mid- and hind-limbs are set close to the centre of gravity of the insect, in the optimal position for steering, and they are rotated so that the coxae and the limbs are horizontally inclined. An analysis of the rowing movements (see below) has shown that this is an adaptation towards life on the water-surface which

tensor ; EM., epimeron ; ES., episternum ; FW., fore-wing ; FWS., fore-wing sclerites ; HW., hind-wing ; HWS., hind-wing sclerites ; LO., lateral occipital muscle ; LPr., lateral trochantinal protractors ; LS., lateral scutal area ; LT., latero-tergite ; M., metatergum ; MG., mesophragma ; MP., mesophragmal pit ; MPr., median trochantinal protractor ; MS., median scutal area ; O., omphalium ; P., pronotum ; PA., pre-alary sclerite ; PAP., pleural apophysis ; PG., prephragma ; PGM., prephragmal muscle ; PL., pronotal lobe ; PSP., post sternellar plate ; PST., post scutellum ; R., limb retractor ; S., scutum ; SA., sternal apophyses ; SAM., sternal apophysial muscle ; SF., supra-coxal flange ; SO., sterno-occipital muscle ; ST., scutellum ; T., tergum ; TM., trochantinal muscles ; TO., tergo-occipital muscle ; Tr., trochanter ; TS., thoracic spiracle ; VA., ventral apodeme tensor ; W., wing bases.

leads to a loss of efficiency on land. When placed on a solid substratum these insects either progress by a series of uncontrolled leaps, or walk slowly and awkwardly by the normal ' tripod ' method of most terrestrial insects.

Both the fore- and hind-wings are recognisable as rudiments in *G. najas* which is predominantly apterous (Brinkhurst, 1959 a). These wing rudiments lie completely beneath the pronotal lobe in life, and are seen only when this is removed (Fig. 5D). The wing venation cannot be discerned, and cannot therefore be compared with the figures given by Hoke (1926). Accessory sclerites are usually present though they may vary in shape, one form being illustrated in Fig. 5D. There are three sclerites in the fore-wing base, the first is associated with the prealary wing process and is generally small. The second sclerite forms the base of the wing and is broadly triangular, whilst the third is of characteristic form, lying along the inside of the wing base medially. It has a triangular base and a narrow projection running beneath the wing posteriorly. The hind-wing sclerites, also three in number, are less easily visible and also more variable. The median sclerite encompasses the base of the wing as a deep U-shaped patch. The first and third sclerites are long and thin and lie parallel to the wing. Comparison with the sclerites in *G. lacustris* (Guthrie, 1954) shows that they are reduced in *G. najas*, a flightless species, an observation similar to that made by La Greca (1949) for *Pyrrhocoris apterus*.

The first thoracic spiracle is situated beneath a lateral fold of the prothoracic lobe between the pro- and mesothorax. The opening is controlled, a single muscle pulling on two valves, one of which is fused to the post spiracular plate, the other more anterior valve receiving the insertion of the muscle. The second thoracic spiracle is similar in form lying horizontally on a lobe above the supra-coxal flange of the mesothorax. The single muscle is posterior, originating on the mesopleural apophysis and again inserting on one valve of a pair controlling the aperture. No separate sclerite could be seen associated with the immovable valve.

Thoracic muscles

In each segment of the thorax the following muscles concerned with locomotion may be identified. The main retractor of the limb is a large muscle originating on the tergal, pleural and (except in the prothorax) sternal areas. It inserts in each case by means of a large tendon and a triangular plate on the posterior edge of the trochanter (Figs. 5E, F). These muscles act horizontally in the mesothorax and metathorax in order to produce a corresponding movement of the leg. The muscle has to be elongate in order to be able to contract by an amount capable of moving the trochanter through as wide an angle as possible, and its insertion on the fulcrum of the limb means that this movement is greatly magnified by the considerable length of the leg. Inserted on the base and shaft of the retractor tendon are the accessory tendon muscles, originating on the inner or posterior half of the coxal walls. One group of fibres is inserted on the lateral edges of the sclerotised plate which joins the trochanter and the tendon. The other more median muscle is inserted on the tendon itself. In the mesothorax another small slip inserts on the tendon from an origin on the sternal apophysis. In each segment the next most prominent

muscles to the retractors are the inner and outer rotators. These originate dorsally on the tergum and act vertically, or slightly more horizontally in the metathorax, and in each case they insert on the inner and outer edges of the coxal rim by means of a sclerotised plate. Associated with the coxal base in each segment are two further muscles, the first inserting in the trochantinal sclerite from a sternal origin, the second inserting on the coxal rim from its origin on the sternal apophysis.

The three protractors of each limb, all considerably smaller than the retractors, consist of one median and two lateral muscles originating on the anterior end of the trochanter by means of a sclerotised plate. Within the trochanter are three muscles inserted on the femur laterally and medially, but there is little movement at this joint. Each femur contains two femorotibial muscles, a dorsal protractor and a ventral retractor. There is a single tibio-tarsal muscle ending in a tendon inserted on the proximal tarsal segment and a further small pair of muscles activate the claws via the unguitractor plate.

These muscles may be identified in each segment although they vary in proportion, as for instance in the prothorax where the majority are only moderately developed. The large mesothorax contains the huge retractors referred to above, whilst those of the metathorax are longer than might be supposed, as they follow the forward extensions of the segment on each side of the mesophragma (Fig. 5F). The rotators are well developed in each segment as they are responsible for holding the body of the insect clear of the water surface, as well as being used in leaping.

In winged species the large, indirect wing-muscles are found only in the mesothorax. The horizontal muscles run from the anterior face of the mesothorax to the mesophragma, whilst the vertical muscles run from the sternum to the membranous scutal areas of the mesonotum, both medial to the limb muscles. The mesothorax is a rigid box with a thin roof, which responds to the movements of the indirect wing-muscles, transmitting their movements to the wings. This explains the need for the protective pronotal lobe, and also the shape of the metatergum, which has the hind-wing bases on its forward projections. The hind-wings are thus brought close to the fore-wings, where movement will be induced via the mesonotum in the absence of metathoracic wing muscles. The value of these forward prolongations in regard to the limb muscles has already been described.

Rowing mechanism

The rowing movements of various surface-skaters, both adults and nymphs, were investigated by means of a film as described above. Figure 6 shows six consecutive frames of a film made of the movements of a fifth instar *G. najas* nymph. The legs are shown in the resting position in Fig. 6A, whilst Figs. 6B–F show one complete stroke. Two points emerge from a study of this figure. The first is that, contrary to the views expressed by Pratt (1938), both mid- and hind-limbs participate in the rowing stroke, not the mid-limbs alone. From the size of the mesothoracic limb retractors and the large angle through which this limb moves it is probably true to say that this segment produces the greater part of the locomotary thrust. Pratt (1938) and others

held that the hind-limbs were responsible for steering the insect, but it now seems more likely that this is achieved by unequal contractions of the mesothoracic retractors of either side exerting a greater thrust on one side. When at rest a pond-skater often turns by moving only one mesothoracic limb, so that unilateral movements are possible.

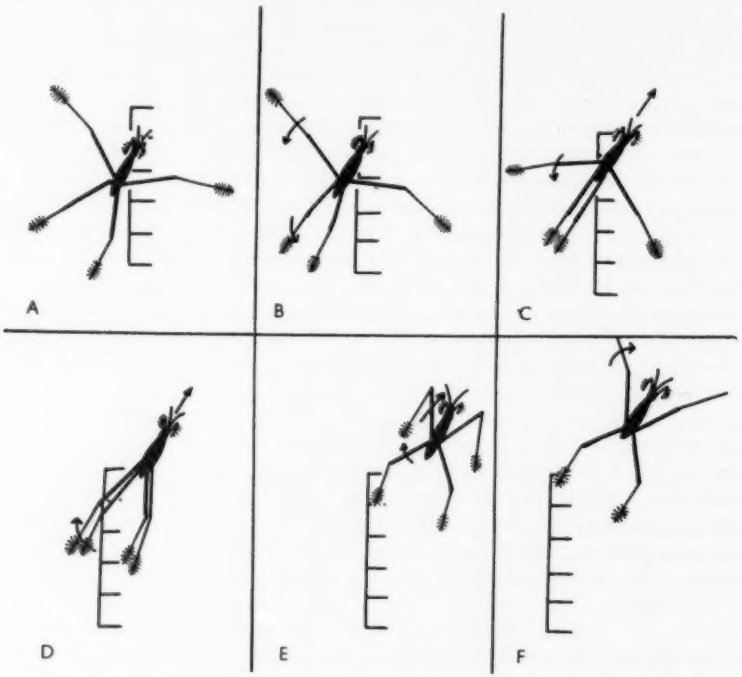

Fig. 6.—Six consecutive stills from a film of *Gerris* rowing.

The second feature of interest concerns the recovery stroke—to what extent does the insect " feather " its legs on the return stroke ? Reduction in frictional drag could be achieved in two ways, either by trailing the tarsi so as to present its long axis to the path of motion, or by lifting the mesothoracic limb clear of the surface, and balancing on the fore- and hind-limbs. It appears that both these mechanisms are employed. The limb is first protracted with the tibiae and tarsi trailing and then this distal part of the limb is lifted and swung rapidly forward off the water surface. This is seen in the film by the limb going out of focus at this stage of the movement cycle, and is indicated in Fig. 6F by the absence of haschures denoting the depression of the surface film where a limb is in contact with it.

Rowing constitutes one of three alternative ways of progression other than flight in these insects. On solid substrata they may walk in the normal

'tripod' manner or may leap by means of the combined action of the limb retractors and rotators. Any attempt to slow down the rapid swimming movements by placing them on fluids of high density results in the adoption of one or both of these alternative methods of locomotion.

The actual physical means by which the movements of four isolated tarsi on the water surface produce a forward thrust is not at all clear. It is possible that the surface film becomes "packed-up" behind each tarsus during the rowing stroke and the resulting build-up of surface pressure imparts a forward thrust. It is interesting to note in this context that *Velia* seems to have some extension of the normal mechanism. If an individual is placed on a fast-flowing stream (either in the field or on an artificial stream in the laboratory—Brinkhurst, 1958) such that the limbs are rowing apparently as fast as they are able but no progress is made against the flow, an odd phenomenon is observed. The limbs, having rowed extremely fast for a while, stop altogether but instead of being immediately swept downstream the insect moves forward at an extremely rapid pace, apparently effortlessly. This forward movement appears so suddenly and is so fast compared with normal rowing speeds that it might be compared with the surface-tension lowering mechanism in *Dianous coerulescens* Gyll. (Jenkins, 1957), but no anatomical evidence can be found to support this.

Short-winged forms of polymorphic species have been shown to lack the large indirect wing muscles which occupy a considerable volume of the meso-thorax in winged forms. There is thus a saving in both space and available protein in flightless forms, as, though it is true that the thorax of a short-winged is smaller than that of a long-winged form of the same species, this difference is not enough to compensate fully for the absence of the wing muscles. Many theories of the significance of alary polymorphism have been more concerned with this extra space than the loss of flight involved, and most of these will be discussed elsewhere (Brinkhurst, 1959a).

One view is that the extra protein and space available leads to an increase in size (and hence the cross-sectional area) of the mesothoracic limb retractors, and that by this means the selective advantage of the short-winged forms lay in their enhanced rowing ability compared with the long-winged forms. This hypothesis is here tested experimentally by the method described above. The results refer to the total frequencies for ten individuals of two polymorphic forms of *G. lacustris* (macropters and brachypters), each individual being employed for the first twenty attempts at rowing and then discarded. Five insects escaped or were damaged before the twentieth observation could be made and so 196 observations were made on brachypters, 194 on macropters. Students t test on these results gave $t=0{\cdot}43$, where $n=388$ therefore $p=0{\cdot}7$, and so the null hypothesis (that there is no significant difference in the rowing ability of these two forms) is accepted. A further experiment was carried out to demonstrate that the apparatus was capable of showing differences in rowing ability where these existed. A female *G. najas* (one of the two largest British gerrids) was employed in the same apparatus but it was found that the weight required to obtain a similar table of results was 22 milligrams compared with that of 3 mgm. used in the case of *G. lacustris*. This was taken

TABLE 1

The frequency with which a weight was lifted past a graduated scale by macropterous and brachypterous *G. lacustris* (females).

Scale readings in cms.	2·0–3·5	4·0–5·5	6·0–7·5	8·0–9·5	10·0–11·5	12·0–13·5	14·0–15·5	Total
Brachypters	55	54	36	32	17	2	0	196
Macropters	62	50	29	24	19	6	4	194
Difference	–7	4	7	8	–2	–4	–4	

to demonstrate the validity of the test in view of the morphological evidence which showed that the retractor muscle of the mesothoracic limb was very much larger in *G. najas* than that in *G. lacustris*.

From the above observations it is difficult to see how the significance of short-winged forms in mixed populations could be attributed to their ability to row faster than the macropters.

Reactions to changes in surface tension

Walton (1943) suggested that differences in the surface tension on natural water-bodies might be important in determining the habitats of the various species of surface-dwelling Heteroptera and gave a few observations on the reactions of *Gerris* to artificially produced variations in surface tension. His method was not described in any detail and therefore a new method was evolved to test this hypothesis. This was described above. The results of these experiments showed that all adult gerrids were sunk by about the same degree of lowering of the surface tension (Table 2) and that this " limiting value " lay below the values commonly recorded in the field (Goldacre, 1949). From this we may deduce firstly that surface tension is only important in that it excludes all species from rare, extremely polluted habitats and secondly that there is some compensation for the increased weight of larger species as the limiting value/weight relationship is approximately constant (Table 2). China (1955) expressed the view that the increase in the length

TABLE 2

The relationship between the limiting value of surface tension and the mean weight in *Gerris* and *Velia*.

Species	Limiting value of surface tension (Dynes/cm.)	Mean weight in milligrams
G. najas adult	44·9	45·5
Instar 1	50·8	0·6
G. argentatus	41·1	7·1
G. odontogaster	45·4	10·4
G. lacustris	43·8	12·6
G. gibbifer	39·7	15·0
G. thoracicus	42·3	18·3
V. caprai	36·6	10·0

of the leg in larger species compensated for the increase in weight by distributing this over a wider area. This statement is true only of the length of the tarsus and distal end of the tibia however as these are the parts of the limb which normally contact the water. It was noticed that as the limiting value of surface tension was approached, more and more of the tibia contacted the water-surface and this may be regarded as the method by which temporary changes in the strength of the surface film are overcome.

THE METASTERNAL GLAND

China (1955) laid considerable emphasis on the modifications of this gland in surface-dwelling Heteroptera, illustrating a series of stages between the condition described by Brindley (1930) in most terrestrial Heteroptera and that in *Gerris*, where the normally paired apertures of the single median reservoir have moved into a median position and fused to form the omphalium. Internally, the structure has remained largely unmodified, the paired glands opening separately into the median reservoir, which bears the accessory gland on its dorsal surface (Fig. 7). The histological structure and the nature of the controlling mechanism resemble those described by Henrici (1940) in a number of terrestrial Heteroptera and Kemper (1929) in *Cimex*.

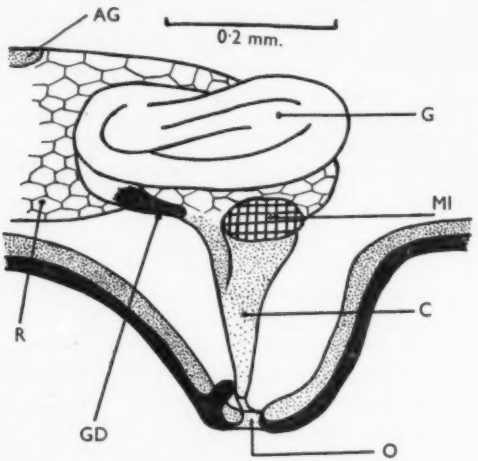

Fig. 7.—Metasternal gland. AG., accessory gland ; C., channel from reservoir to exterior ; G., gland (right side) ; GD., duct from gland to reservoir ; MI., muscle insertion ; O., median aperture in omphalium ; R., reservoir.

The primitive condition of this complex may be visualized as one in which each gland has its own reservoir so that there are two independent lateral systems opening beside the metathoracic coxae, as in many Reduviidae. China (1955) has shown that some primitive water-skaters (Hebroveliidae, *Ocellovelia*, *Heterocleptes*) retain the dual openings, although these are in a more median position than usual, and have channels leading from them to lateral

evaporation areas. *Velia*, *Brachymetra* and *Cylindrostethus* have a single median aperture as in *Gerris* but retain the channels.

Whatever the functional reasons for the adoption of a median aperture combined with channels to take the secretion back to the original lateral position, it seems possible that there has been some alteration in the function of this gland in *Gerris*. These insects are the most highly modified for rowing over the water surface of any Gerroidea, and thus progression over solid substances is difficult. The insects are unable to keep the ventral areas off the ground and so it is likely that the original waterproofing wax-layers are removed, especially during overwintering. The waterproofing qualities of the ventral hydrofuge pile are of considerable value to the insect (as shown above in the experiments on surface tension) especially during oviposition (see below). It is conceivable that the single aperture with its muscular control permits an increase in the volume of the secretion liberated at discrete intervals, which may be used to produce an oil film on the pile.

In a preliminary experiment on the function of this gland, twenty male *G. najas* were placed in small glass refrigerator dishes containing different substrata. Five insects were placed in dishes containing water, and five in dishes with a lump of wet cotton-wool. These acted as controls to be compared with insects kept on sand (on which the wax layers might be expected to be removed) and others again with cotton-wool, but in this case the ventral surface of each insect was wiped with cotton-wool soaked in ethyl acetate to

TABLE 3

Results of experiments on the function of the metasternal gland in *Gerris najas*.

Substratum	Size of reservoir (mm.)	State of reservoir
Water	0·8	Full
	0·8	Full
	0·85	Full
	0·9	Full
	0·95	Full
Glass with damp cotton-wool	1·0	Full
	1·0	Full
	0·85	Full
	0·85	Half full
	1·0	Full
As above, but wiped with ethyl acetate	0·2	Empty
	0·85	Full
	1·0	Empty
	0·85	Empty
	1·0	Half full
Sand	0·5	Empty
	0·75	Empty
	0·85	Empty
	1·0	Full
	1·2	Full

remove the wax chemically. The insects were kept for five days, during which they were fed on *Tenebrio* larvae, and at the end of this time they were killed in ethyl acetate vapour, and dissected in 70 per cent alcohol. The size and condition of the reservoir was noted and the results are detailed in Table 3.

In the two cases where the wax layers might be expected to be removed most insects had empty, or partially empty, reservoirs, as judged by observations on the dissections. The size of the reservoir does not seem to correspond to the quantity of fluid contained. The many other gerrids dissected for other purposes have all been seen to have the reservoir in the turgid condition and this fact was noted by Brindley (1930). It is therefore conceivable that waterproofing forms at least part of the function of this gland in *Gerris* although a distinct and slightly unpleasant odour is discernable.

THE REPRODUCTIVE SYSTEM

Introduction

Previous studies on the structure and homologies of the genitalia in the Heteroptera have been chiefly concerned with hard parts observed *in situ* (Poisson, 1940). The male organs of *Rheumatobates* were described by Schroeder (1931) in the half-expanded condition, employing the terminology adopted by Singh-Pruthi (1925). The female organs were described by Snodgrass (1935) and the terminology used here follows his account somewhat modified after discussion with Scudder (p.c.). A new terminology was erected by Dupuis (1955) which has not been widely accepted as it was not backed by many fresh observations. The spermatheca was described first by Kerkis (1926) and then by Pendergrast (1957), but a new interpretation of this structure is advanced here from which it is possible to homologise the organ more closely with that of other Heteroptera. The musculature of the genitalia was reviewed by Guthrie (1954).

The male organs

On each side of the abdomen is a pair of testis lobes, each with a short duct which joins that from its fellow to form the vas deferens on each side. Just below the testes the vasa deferentia are expanded to form the vesiculae seminales. The distal vasa deferentia run forward along the vesiculae seminales before turning posteriorly to unite just before entering the eighth segment. The median ejaculatory duct runs along the floor of the basal plate to enter the aedeagus. The copulatory organs lie within the ninth segment being formed in the 9–10 intersegmental membrane (Singh-Pruthi, 1925). When retracted they lie within the eighth segment (Fig. 8B) which is in the form of a short cylinder, the distal end of which is deeply emarginate to expose the ninth sternum. The dorsal aperture in the ninth segment, through which the aedeagus emerges, is covered at rest by the short ninth tergum and the proctiger. It is rimmed postero-laterally by a pair of sclerites (closely associated with the edge of the ninth sternum) termed the parandria (Leston, personal communication). The proximal ends of these two sclerites form hook-shaped supports for the parameres, and form the fulcrum on which the basal plate swings. The parameres are small lobes thinly covered with bristles, and a

narrow sclerite runs forward from each ventrally, becoming the tendon of a small muscle. The basal-plate is a single structure, the two elements being fused. Medially the plate is continued as the basal-plate process attaching to the phallosome (or proximal portion) of the aedeagus itself. The four supports of the basal-plate in other Heteroptera are here represented by muscle insertions (see below). The walls of the aedeagus are variously sclerotised (Fig. 8A). The basal phallosome, which houses the remainder when retracted, is quite strongly sclerotised, and firmly joined to the basal-plate via the process of the latter. Distal to the phallosome is the endosome, which is divided into a short, thin-walled portion, the conjunctiva, and the more distal vesica. In *Gerris najas* the vesica is further divided into proximal and distal portions. The wall of the proximal portion of the vesica is lightly sclerotised ventro-laterally, whilst the distal end of this section is more strongly sclerotised to form a cap which serves to close the distal aperture of the phallosome when the aedeagus is retracted within it. There are three endoskeletal elements in the vesica of *G. najas*, a pair of lateral rods in the proximal portion, and a single median rod in the distal part. The single median rod is hinged on to the paired rods in such a way that it is free to swing through almost 180° from its position (in the retracted state) between them, to its fully erected position as a distal projection (as shown in Fig. 8A). The roof of the proximal portion is thin and closely folded in the retracted condition, the other walls of this part being sclerotised as shown above. As the aedeagus expands the distal endosomal rod swings over dorsally (Fig. 8D), the wall of the vesica unfolding behind it. The only mechanism which could produce this movement of the distal rod in the absence of a muscle is localised distension of the thin dorsal vesica wall due to increase in the body-fluid pressure. Distally, the third sclerite bears a stirrup-shaped aperture through which the final portion of the ejaculatory duct runs having traversed the aedeagus. The termination of the duct appears as though it is itself eversible to form the final extension which reaches the spermatheca.

The eighth segment bears four pairs of muscles, originating in the seventh segment and being responsible for swinging the eighth segment and all parts distal to it into a vertical position below the body (Fig. 8B). From origins on the eighth segment various muscles insert on the ninth segment and the proctiger. From the tergum one pair inserts on proximal extensions of the proctiger lying beneath the ninth tergum ; a second inserting on the ninth tergum itself. These presumably retract the proctiger and the ninth tergum respectively or they may assist the ventral two pairs (the lateral and ventral sternum 9 retractors) inserted on the ninth sternum in retaining the latter within the eighth segment. This segment is thrust out of the eighth by body-fluid pressure prior to copulation. The basal plate is rotated about the parandria by two pairs of muscles, both of which originate on the ninth sternum, one inserted above, and one below, the fulcrum (the levator and depressor basal-plate). The small paramere muscle inserts on its articulatory sclerite.

When the eighth segment has reached the vertical position the basal-plate is lifted, elevating the aedeagus by means of the basal-plate process. The endosome is then everted by body-fluid pressure until the final segment is

clear of the phallosome. By this time the aedeagus is lying over the right-hand side of the ninth sternum, extending horizontally forward (Figs. 8A, 8D). The distal end of the endosome unfolds as described above, the whole then being received by the vaginal chamber of the female. The distal portion of the ejaculatory duct probably everts to reach the spermatheca.

This 180° revolution of the aedeagus is necessary because of the position adopted in copulation, when the male seizes the females from above, clasping the mesothorax with his fore-limbs, and, in the case of *G. najas*, retaining this position for considerable periods, rowing about with the female although not often actually copulating. Even transport of specimens all day in tubes does not break the continuity of this behaviour although other species are more easily separable. The whole process of erection may often be brought about by the high pressure which ensues when the living insects are immersed in hot water ; sometimes an additional pressure on the abdomen is necessary.

The erection of the aedeagus in other *Gerris* species is illustrated in Fig. 8C where it can be seen that, in contrast to *G. najas*, the vesica is divided into three parts. The process follows the above description with the addition of the extension of the fourth endoskeletal rod, which is held folded back along the third sclerite at rest. It is significant to note that the two species in the sub-genus *Hygrotrechus* (*najas* and *paludum*) differ in this repect as well as in life cycle and polymorphism (Brinkhurst, 1959a) and so the view expressed by Poisson (1924) that these two species had recently separated from one original polymorphic species by both sexual and geographic isolation cannot be maintained.

The female organs

The ovaries consist of four ovarioles on each side which lie entirely within the abdomen when immature. When mature the eggs are so large that they fill all the available space in the meso- and metathorax, replacing the wing muscles in winged species. Three or four eggs are found in each ovariole in most *Gerris* species, but *G. najas* has six or more, and even the greater size of this species is insufficient to compensate for this increase in the number of eggs, which therefore distend the abdomen so far as to separate the terga and sterna. The eggs are described below.

The two oviducts unite to form a wide chamber into which open the vagina and the spermatheca (Fig. 8E). A hitherto undescribed part of the latter, a small terminal bulb, lies embedded in the median anterior muscle inserted at the point of union of the two oviducts. This muscle originates on a median apodeme arising from the anterior border of sternum seven, which projects well forward into the sixth abdominal segment. A thin, coiled duct runs through the muscle from the terminal bulb to the pump of the spermatheca, a large structure with a sclerotised ridge on to which are inserted a pair of muscles originating laterally on segment seven. A widely undulating tube runs from the pump, and opens into the dorsal wall of the vagina. Opening at this point also is a long coiled accessory gland. Pendergrast (1957) called this gland the spermatheca, but made no reference to the terminal bulb, interpreting a portion of the duct leading to it as a fecundation canal. The nature

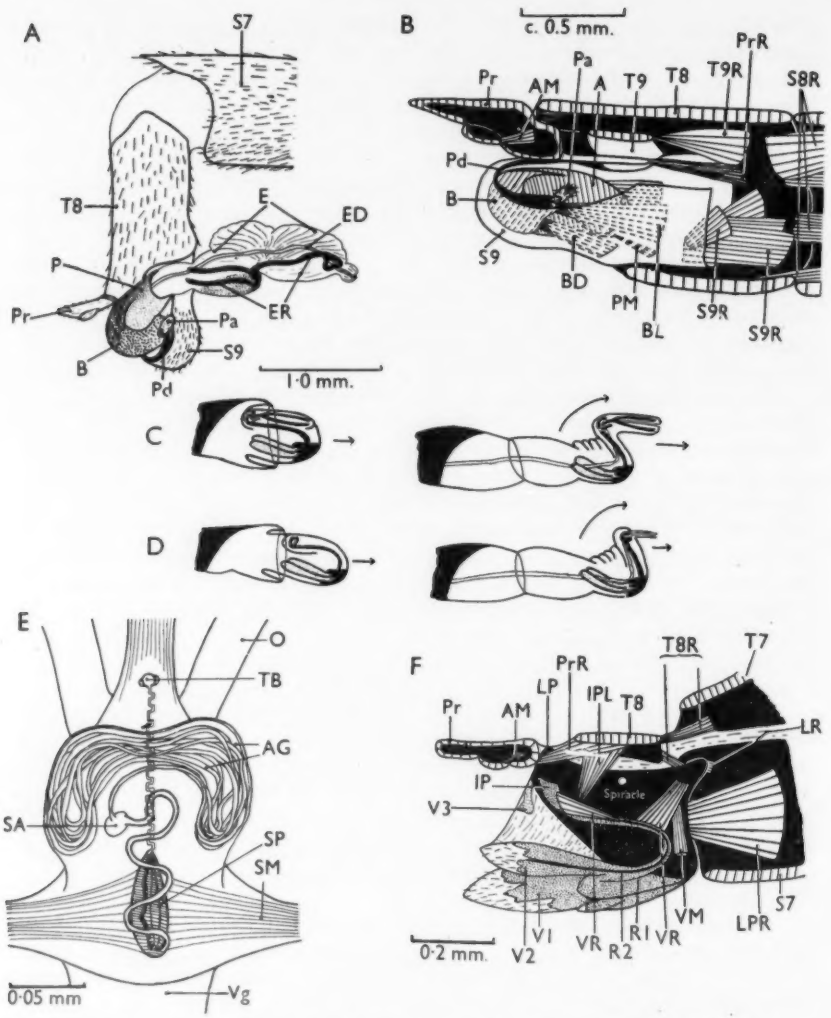

Fig. 8.—The reproductive system. A. Male organs, erected ; B. Diagrammatic sagittal section of the male genitalia ; C. Erection of the genitalia of other *Gerris* species ; D. Mode of erection of the genitalia of *G. najas* ; E. The spermatheca ; F. Diagrammatic sagittal section of the female genitalia.

A., aedeagus ; AG., accessory gland ; AM., anal muscle ; B., basal plate ; BD., basa plate depressor ; BL., basal plate levator ; E., endosome ; ED., ejaculatory duct ; ER., endoskeletal rods ; IP., inner plate ; IPL., inner plate levator ; LP., lateral plate ; LPR., lateral plate retractor ; LR., lateral plate rotator ; O., oviduct ; P., phallosome ; Pa., paramere ; Pd., parandria ; PM., paramere muscle ; Pr., proctiger ; PrR., proctiger

[*Continued bottom of next page*]

of the coiling of the duct suggests that it is straightened as the muscle in which it is embedded is contracted, pulling the whole spermatheca forward and at the same time occluding the apertures of the oviducts so that insemination takes place in the proximal tube of the spermatheca. Pendergrast (1957) stated that " the spermatheca of the Gerridae, Veliidae, Hydrometridae, Mesoveliidae and Hebridae however differs fundamentally from all others in the Heteroptera. The presence of a second duct (the fecundation canal) . . . is unique in the sub-order ". It has been shown above that the so called " fecundation canal " terminates in a small bulb. The spermatheca in *Gerris* may therefore be closely homologised with that in the Geocorisae Trichophora, where there is in the spermatheca a terminal bulb and a muscular pump. This structure is distinct in *Gerris*, however, in that the terminal bulb is small and separated from the pump by a thin duct, and also there is a large accessory gland (the spermatheca of Pendergrast). The eggs (see below) are laid in a jelly-like matrix in *Gerris* which may be derived from this gland, although the gland is well developed in *Mesovelia* which inserts its eggs into plant stems.

The ovipositor is reduced in Gerroidea, but the valvulae and valvifers described in other Heteroptera by Snodgrass (1935) are readily discernible. The eighth tergum is a single dorsal plate anterior to the proctiger (Fig. 8F). Latero-ventrally lie two sclerites, each bearing a spiracle, with which the valvulae articulate, and these are therefore homologous with the eighth paratergites and first valvifers fused (henceforth called the lateral plates). The first valvulae are blade shaped, articulating by a basal, triangular sclerite with the lateral plates. Between the first valvulae are two narrow sclerites united by a membrane along their basal two-thirds. The processes arising on the first valvulae are termed the first rami. These curve dorsally and attach to a second pair of sclerites (termed the inner plates) probably the ninth paratergites and second valvifers fused, as the rami of the second valvulae are associated with them. The second valvulae lie within and above the first and are similar in shape. The second rami lie in grooves formed by the first pair, their distal ends being attached to the inner plates by short muscles. Between the second valvulae and the inner plates, and below the proctiger, is a large membranous area which becomes the roof of the chamber formed when the genitalia are erected, and in this membrane lie two patches of sclerotisation which, from their position, would appear to be the third valvulae of Snodgrass (1935) termed the ninth terga by Guthrie (1954).

The largest muscle of a series associated with the female genitalia is inserted on the upper lateral surface of the lateral plates, and originates ventrally on the seventh sternum (Fig. 8F). This muscle retracts the lateral plates from the vertical position adopted in copulation. A number of short muscles are associated with the dorsal anterior prominences of the lateral plates. On the outer side of each plate are the insertions of a series of muscle fibres with the proctiger retracted by its muscle.

retractor ; R., ramus ; S., sternum ; SA., aperture of spermatheca ; SM., spermathecal pump muscle ; SP., spermathecal pump ; S8R., S9R., sternal retractors ; T., tergum ; TB., terminal bulb of spermatheca ; T8R., T9R., tergal retractors ; V., valvula ; VM., vaginal muscle ; VR., retractor valvulae ; Vg., vagina.

As in the male, the chief erecting force is body-fluid pressure, presumably produced by the tergo-sternal muscles of the abdomen aided by protractor muscles which are notably smaller than the corresponding retractors which have their origins on the base of the lateral projections of the seventh segment. These are the rotators of the lateral plates. A second pair of muscles run from the lateral plates to the eighth terga laterally (the tergal retractors). On the inner side of each lateral plate prominence are two further muscles. The first runs ventrally to insert on the vagina, and the second, large, muscle inserts on and retracts the ramus. A small muscle (the retractor of the second valvulae) is inserted on each inner plate from the second ramus. A pair of muscles inserted on the inner plates from the eighth tergum act as the protractor valvulae, and a small muscle inserts in the eighth tergum from the seventh on each side. The only other muscles are those homologous with the proctigeral muscles of the male.

During erection of the genitalia the lateral plates are erected by the short rotators, probably assisted by the lifting of the eighth tergum by the muscles attaching this to the seventh segment. Then body-fluid pressure acting on the folded membranous area above and between the valvulae forces these to be protracted, the second moving forward in the grooves of the first valvulae. This may be aided by the dorsal muscle inserting on the inner plates, lifting these and thus protracting the valvulae. Retraction of the genitalia is effected by the large retractors of the lateral plates, valvulae, and inner plates respectively.

Oviposition

Considerable uncertainty as to the site of oviposition is expressed in many accounts although some suggest that at least a proportion of the eggs are laid beneath the water, Wesenberg-Lund (1943) describing groups of fifty eggs laid in jelly on *Potamogeton* leaves. The same account refers to the eggs of smaller species of pond-skaters as being laid singly or in small groups on plant stems, rolled leaves or in moss. Liche (1936) described the nymphs of *G. najas* as sinking below the water-surface on hatching (presumably from eggs laid above the water) and later rising back through it.

Many species of *Gerris* have been induced to lay eggs in captivity, and in all cases they were fixed to a solid object (the sides of the container or wooden blocks provided for the purpose) in a jelly-like matrix just below the level of the water. These eggs only hatched if kept beneath the water surface ; all nymphs hatching above the surface film were damaged and drowned. The eggs of *G. najas* were observed on several occasions in the field ; they were always beneath the water, usually on stones on the lake bottom. They are laid in discrete groups, often comprising as many as thirty-seven though the mean number per batch in twenty-four batches was 21·1. The majority of mature female *G. najas* contained forty-eight eggs (the mean of seventy-nine individuals) and so it appears that these insects survive their initial journey beneath the water, the data implying that two batches of eggs are laid.

One female was observed walking below the water-surface in a tank filled with stones to above the water level. This occurred in a darkened laboratory

and it has also been observed that pairs of *G. najas* only separate in the dark and so it seems that oviposition takes place at night. Females forcibly submerged beneath gauze in aquaria regain the surface after at least two hours submersion, presumably respiring through the air-bubble trapped in the pile on their ventral surfaces. Females wetted with detergents sank immediately and died rapidly, the waterproof pile being destroyed.

The process of oviposition was observed once in daylight. A female *G. argentatus* was observed to push the fore-limbs through the surface whilst clinging to a block of wood. The abdomen was drawn beneath the water, and the ovipositor was rubbed over the surface of the wood until a site was selected, whereupon the bug sat quiescent for about half a minute. The whole egg appeared suddenly but the insect did not move for fully a minute. Then the abdomen was jerked off the egg, which remained firmly adhering to the wood. Presumably the abdomen remained in contact with the egg for long enough to ensure that the jelly-like matrix had set. Only the eggs of *G. najas* have been observed in the field but it seems reasonable to assume that they are laid at or beneath the water surface in most other species, possibly on the stems of aquatic plants. The vegetation amongst which these insects have been collected was frequently examined but no eggs have been observed.

The eggs and development

The eggs of *G. najas* are oval in shape, and about 1·8 mm. long. When first laid they are light grey, but within twelve hours they darken and turn yellow-brown. As development proceeds they gradually darken further and the red eye-rudiments soon become obvious. The most unusual feature of the development is the complex coiling of the long mid- and hind-limbs, the former running posteriorly on the ventral side and coiling around the abdomen before traversing both the thorax and the abdomen dorsally. The limbs may be followed out in detail in Figs. 9B–C, as they are labelled as follows :—

right mid-limb	x–y, y–z	left mid-limb	x′–y′, y′–z′
right hind-limb	1–2	left hind-limb	1′–2′.

Nymphs emerge from the egg with the aid of a conspicuous egg-burster which is left behind along with a thin pellicle after emergence (Fig. 9A). The nymphs often rise directly to the surface, but may remain submerged for a period. The nymphs of the British *Gerris* species will be described (Brinkhurst, 1959b).

DISCUSSION

China (1955) discussed the changes involved in the adoption of life on the surface film of water, and we are now in a position to understand the functional significance of some of these. The head is largely unmodified in this genus which feeds in much the same manner as terrestrial carnivorous Heteroptera. The prothorax apart from the pronotal lobe is also comparatively unmodified, but the rest of the thorax shows many significant differences. The muscles of the prothorax act vertically as is the case in most walking-legs in insects, and so this segment is of normal length. The mid- and hind-limbs both act

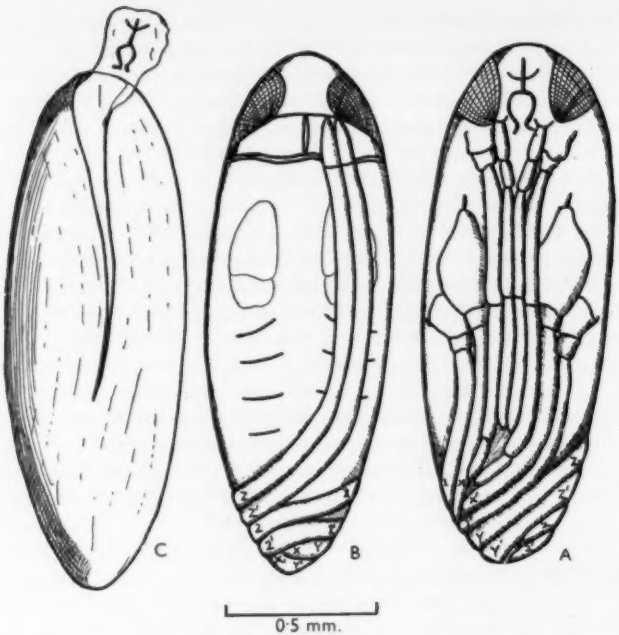

Fig. 9.—A and B. Ventral and dorsal view of the egg just prior to hatching ; C. Egg after hatching.

horizontally in rowing and so are inserted laterally and have the retractor muscles in a horizontal position. Both these segments have become elongate to house these enlarged horizontal muscles, the elongation of the metathorax being restricted to the dorsal part of the segment and therefore not immediately obvious. The whole thorax is braced by the endosketal elements described above. The roof of the mesothorax is however thin and membranous, movements being induced in this by the indirect wing muscle in alate forms. This movement is transmitted to both pairs of wings in the absence of metathoracic wing muscles. The hind-wing bases are situated on forward prolongations of the metatergum. Therefore the mesothorax forms a thick-walled box with a thin lid, and this is protected by the posterior expansion of the pronotum termed the pronotal lobe. It is the elongation of the mesothorax which is an adaptation to life on the water surface and only indirectly is this true of the pronotal lobe, contrary to the views expressed by China (1955). This lobe therefore persists in flightless forms and is not restricted to the winged forms (China *loc. cit.*).

The elongation of the limbs is an adaptation to rowing and not to the distribution of the insect's weight over a wider area of the surface (China *loc. cit.*) as each limb bears one-sixth of the total body weight wherever it is placed so long as the depressions made in the surface film do not co-alesce. Increase in

the surface area of the tarsus however probably compensates for the increased weight of the larger species as the relationship between weight and " limiting-value " of the surface tension is constant. There seems to be no significant difference in the rowing ability of two polymorphic forms of *G. lacustris*.

These insects would be unable to maintain their position on the surface if the tarsal claws were not modified as these would penetrate the film immediately. One would not therefore be surprised to find that the claws were absent, but instead it can be seen that they are retracted into sub-apical grooves in the adult, which position is maintained whilst the insects row. It has been shown above that the females deposit their eggs below the water-surface and observations in the laboratory suggest that the initial penetration of the film is carried out by the fore-tarsal claws. Also it is shown elsewhere (Brinkhurst, 1959a) that *gerrids* overwinter on land and so the claws are retained for these purposes, the tarsus being modified towards life on the water-surface. Both the thorax and the abdomen are covered by a hydrofuge pile which prevents the insects from being wetted, possibly assisted by the metasternal gland. The pile also enables the insects to respire if submerged, and this is used by the females during oviposition, when they migrate below the water surface. The ovipositor is reduced in these insects which do not insert their eggs into plant stems, but the accessory gland of the spermatheca is enlarged. It is thought that this provides the jelly-like matrix in which the eggs are laid and which serves to cement them to solid objects beneath the water.

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SUMMARY

Various aspects of the morphology of *G. najas* are described from a functional viewpoint, and experimental evidence is used to support some of the conclusions reached. Special attention is focused on the structure of the hypopharynx and the associated structures, and the function of the mandibular muscles is reassessed. The thorax is considered as a functional unit in relation to locomotion, and experiments on the mechanism of rowing, with its significance in regard to alary polymorphism are described. The reactions of *Gerris* species to surface tension are investigated. Preliminary observations

are made on the function of the metasternal gland in this genus. The structure and function of the reproductive system in both sexes are discussed, with some observations on the eggs, oviposition and development. A new interpretation of the spermatheca is presented. Many aspects of the morphology are shown to be adaptations to life on the surface film of water.

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THE FOOD OF A SAMPLE OF CROCODILES (*CROCODILUS NILOTICUS* L.) FROM LAKE VICTORIA

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INTRODUCTION

It was shown by Welman & Worthington (1943) that the diet of crocodiles depends very much on their size ; and Cott's more extensive investigations (1954) have confirmed this. Summarising present knowledge of diet in relation to size, Cott presented an analysis of 173 stomachs of crocodiles from various parts of East and West Africa. His general conclusions were that insects formed the principal food of small crocodiles below 2 metres in length, but that amongst larger individuals first fishes and later birds and mammals were of greater importance. In view of these findings it is clear that any further records of stomach contents will be of interest, particularly if they can be correlated with the sizes of the crocodiles. In fact the value of such records increases continually, as it becomes possible for more of the food organisms to be identified.

MATERIAL

In May and June, 1956 Mr Erich Nowotny visited Jinja on a crocodile-hunting safari and allowed me to examine the stomachs of the specimens he shot. In this way I was able to obtain food-records for sixty-four crocodiles. With these I have included records for three other crocodiles shot by Mr D. J. Garrod—sixty-seven in all. These specimens all came from Lake Victoria, in or near the mouth of Napoleon Gulf, within a few miles of Jinja. Nearly all of them were shot at night as they lay at the surface amongst water-lilies in sheltered, muddy regions of the lake. I therefore consider it justified to combine these records for purposes of stomach analysis, since all the individuals probably had access to similar feeding grounds.

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Records from two other crocodiles are presented separately. One specimen was found in a fishing-net in the Albert Nile at Rhino Camp, and the other was caught by Jaluo hunters off Dagusi Island, Lake Victoria, on a double-hook baited with *Tilapia*. Dates of collection of all crocodiles are given in Appendix I. The Dagusi Island specimen was caught in a relatively exposed, rocky region of the lake shore, and therefore is better considered separately from the Napoleon Gulf material. The White Nile at Rhino Camp is wide, muddy and slowly-flowing, with papyrus and grass swamp lining its margins.

METHODS

Crocodiles were measured from the tip of the snout to the tip of the tail, before removal of the skin—a procedure which can shorten the tail. Measurements are given to the least whole centimetre.

In small specimens the stomach was removed intact, but in large ones it was emptied *in situ*. Following a suggestion made by Dr H. B. Cott, the stones which occurred in most stomachs were recorded and weighed. They were separated from the rest of the stomach-contents by panning, and then weighed to the nearest 0·1 gram. In some cases, suitable containers in which to bring back the stones were not available, and therefore it has simply been recorded that stones were present. Most of the stones consisted of quartzite or laterite, and therefore could have been derived from Napoleon Gulf, where outcrops of both types of rock exist.

Part of the contents of seven stomachs (Nos. 7, 9, 13, 20, 25, 26 and 31) were accidentally thrown away, after having been set aside for closer examination ; but these records are nevertheless included, because the preliminary notes which had already been made give an indication of the food. Contents of these stomachs are, of course, omitted from the analysis in Table 1, since they are not directly comparable with the rest.

RESULTS

In any analysis of results of this kind, the conclusions drawn will depend to a great extent on the size-groupings adopted. In the present analysis I have used the size-groupings adopted by Cott (1954) ; but in view of the relatively small size of my sample, I consider it worthwhile also to give the records in full, and therefore these are listed in Appendix I. This gives a more accurate idea of the feeding habits of the specimens concerned, and provides information on the numbers and sizes of the animals eaten—facts of importance in food-chain studies. It also enables these data to be analysed in a different way in future if so desired.

In Appendix II is a list of the names and classification of the animals referred to in abbreviated form in Appendix I.

Analyses of the raw data appear in Tables 1 and 2. The food-types recognised include all those given by Cott. In these tables two values are given per food-type in each size-group. The first records the simple occurrence of a food-type, that is to say the number of stomachs in which it was encountered in that size-group. This statistic is the one most often used in analyses of stomach contents. As a measure of the importance of the food-types eaten,

however, it is open to criticism on the grounds that it makes allowance neither for the size of a food organism nor for its relative abundance. For instance, in a sample of crocodiles each of which had eaten one large lung-fish and also one spider, ' fishes ' and ' spiders ' would receive equivalent scorings, though their relative contributions to the crocodiles' food would have been significantly different.

In an attempt to overcome this difficulty, I have recognised a second category of occurrence, which takes into account the volume of the food present. Thus, if a food-type constituted more than half the total volume of the food in the stomach, it has been termed the ' main contents ' and given a separate scoring. Although subject to certain errors (particularly when there is only a small quantity of food in a stomach), this method of double scoring may be expected to give a much fairer estimate of both feeding habits and food. For instance, in Table 1, size-group 1, we see that Odonata occurred five times as frequently as Mammalia, yet both food-types provided the main contents in the same number of stomachs, namely two, a proportion consistent with the difference in their sizes. Bearing this in mind, we can see that the values for main contents emphasise strongly the importance of insects as food for small crocodiles.

TABLE 1

Number of stomachs containing various food-types

Cott's size-group Length in cm.	1 0–99	2 100–199	3 200–299	4 300–399
INVERTEBRATES	28 (24)	17 (9)	—	—
Crustacea (*Potamon*)	3 (1)	4 (3)	—	—
Arachnida	4 —	1 —	—	—
Insecta	28 (23)	16 (6)	—	—
Hemiptera	20 (12)	9 (4)	—	—
Odonata	10 (2)	6 —	—	—
Orthoptera	6 —	3 —	—	—
Coleoptera	5 (2)	3 (1)	—	—
Hymenoptera	3 (1)	—	—	—
Dermaptera	1 (1)	—	—	—
Mollusca (Gastropoda)	4 —	2 —	—	—
VERTEBRATES	13 (5)	13 (12)	3 (2)	2 (2)
Pisces	5 (2)	10 (8)	2 (1)	2 (2)
Amphibia (Anura)	7 (1)	2 (2)	—	—
Aves	—	4 (2)	1 (1)	—
Mammalia	2 (2)	—	—	—
Nematoda	12	6	—	—
Plant remains	4	4	1	—
Stones	22	22	3	2
Number examined	30	25	3	2
Number containing food	29	22	3	2

In Table 2 the values for food occurrence in Table 1 are expressed as percentages of the total stomachs containing recognisable food in each size-group. Frequencies of Nematoda, plant remains and stones, however, are expressed as percentages of the total stomachs examined. Figures in Table 2 are given to the nearest whole number.

TABLE 2

Percentage of stomachs containing various food-types

Cott's size-group Length in cm.	1 0–99	2 100–199	3 200–299	4 300–399
INVERTEBRATES	97 (83)	77 (41)	—	—
Crustacea (*Potamon*)	10 (3)	18 (14)	—	—
Arachnida	14 —	5 —	—	—
Insecta	97 (79)	73 (27)	—	—
Hemiptera	70 (41)	41 (18)	—	—
Odonata	34 (7)	27 —	—	—
Orthoptera	21 —	14 —	—	—
Coleoptera	17 (7)	14 (5)	—	—
Hymenoptera	10 (3)	—	—	—
Dermaptera	3 (3)	—	—	—
Mollusca (Gastropoda)	14 —	9 —	—	—
VERTEBRATES	45 (17)	59 (54)	100 (67)	100 (100)
Pisces	17 (7)	45 (36)	67 (33)	100 (100)
Amphibia (Anura)	24 (3)	9 (9)	—	—
Aves	—	18 (9)	33 (33)	—
Mammalia	7 (7)	—	—	—
Nematoda	40	24	—	—
Plant remains	13	16	33	—
Stones	73	88	100	100
Number examined	30	25	3	2
Per cent containing food	97	88	100	100

The values for occurrence in Table 1 resemble closely the corresponding figures given by Cott (1954) and confirm the importance of insects as food for small crocodiles, and also the change of diet with size observed in crocodiles of more than 1 metre in length.

My values for percentage occurrence in Table 2 are consistently higher than those given by Cott, but this is because the figures have been calculated in different ways. Had they been computed by the same method, it is very likely that there would be no significant difference between them. Thus Cott (page 4, line 9) states that in size-group 1 *all* of the (46) specimens containing recognisable food had been feeding on insects. According to the method used here, this observation would be recorded as 100 per cent occurrence, a value showing close agreement with that of 97 per cent observed in the present series.

The results given in Tables 1 and 2 and in Appendix I require no further explanation, and I shall therefore only comment briefly on some of the food organisms.

The crabs eaten were almost certainly all *Potamon niloticus* (Milne-Edwards), a species very common on rocky shores at the northern end of Lake Victoria, and the only species so far found in that region of the lake. (A second, smaller species of crab, as yet unidentified, was collected on the exposed, rocky shore at Busungwe, Lake Victoria, near the mouth of the Kagera River, in April 1955, but no specimens are known from other localities.) *P. niloticus* lives amongst rocks and stones near the shore, but has been seen to come out on land.

The species of *Caridina* found in crocodile No. 68 was probably *C. nilotica* (Roux), the commonest species in the Nile in this region.

Pila ovata (Smith), the large gastropod eaten, occurs commonly on rock surfaces just below the water-line.

Spiders of the family Lycosidae, represented here by *Trochosa*, are almost ubiquitous : they are able to run over the water surface, and may occur amongst vegetation near and over water, and under stones on shores. Members of the genus *Dolomedes* (Pisauridae) are also able to run about on the surface-film, and may even submerge when molested.

The skin of the large lung-fish found in crocodile No. 49 had been deeply scored with parallel lacerations, presumably caused by the crocodile's teeth.

The occurrence together of fine sand and feathers in Nos. 37 and 63 suggests that these crocodiles had been attempting to catch birds on a beach, especially since *Gallinula chloropus* often inhabits such places. (This sand was not included in the weights of stones from these stomachs.)

The short brown hair in stomachs Nos. 8 and 66 could not be identified, but it may well have been torn from otters, which form a common prey of crocodiles (Cott, 1954). The Spotted-Necked Otter, *Lutra* (*Hydrictis*) *maculicollis* Lichtenstein, is not uncommon in Lake Victoria near Jinja.

About twenty specimens of the leech, *Haementeria fimbriata* (Joh.), of various sizes, were attached to the inside of the buccal cavity of crocodile No. 64, which was 387 cm. long.

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SUMMARY

1. The stomach-contents of sixty-seven crocodiles from Napoleon Gulf, Lake Victoria, and two from elsewhere in Uganda have been examined. The lengths of all crocodiles were recorded.

2. In recording the results, consideration has been given to the size and abundance of food items, as well as to the frequency of their occurrence. A detailed list of stomach-contents is given, and also brief notes on some of the food organisms.

3. These data confirm previous observations on the food of crocodiles in Uganda in so far as they demonstrate a change in diet with size. In the present series, insects provided the most important food of crocodiles less than 1 metre long, but larger individuals fed to a progressively greater extent on fishes and other vertebrates.

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APPENDIX I

In the following list of stomach contents, the classification given for the prey is the smallest natural group to which identification was possible. Brackets containing an interrogation mark indicate a further stage of identification considered likely but uncertain. Thus ' Pisces (Cichlidae ?) ' records that the stomach contents were *definitely* remains of fishes, and *probably* of cichlids.

To avoid the necessity of frequent reference to the systematic list of prey species in Appendix II, common group names (such as crabs, fishes, etc.) have been inserted before the specific names in Appendix I. Except in crocodile No. 21, the group name " water-bug " always denotes Belostomatidae.

A full stop separates adjacent groups, and a comma adjacent species within a group. The figures after a species show the number of individuals represented. If not in brackets, these frequencies are exact. If in brackets they represent the minimum number of individuals which could have provided the fragments observed. In such cases consideration has been given to size, and to right and left sides of the body.

Estimated dimensions given for crabs represent the greatest width of the carapace, excluding the antero-lateral spines. Estimated lengths given for fishes represent the total length, unless stated otherwise, in which case ' S.L.' indicates the ' standard length ', or the distance between the tip of the snout and the junction of the body and tail fin.

The abbreviations ' M.C.' and ' E.C.' denote the main contents (see text) and entire contents, respectively. The limits of these categories are shown by square brackets.

The stage of metamorphosis reached by Odonata larvae that are eaten can provide an indication of where and when they were caught—a subject to be dealt with in a separate communication. Thus it has been recorded if a specimen was : (a) in the final larval instar ; (b) represented by a larva or by a cast skin (exuvia) ; (c) exhibiting swollen wing-sheaths ; or (d) pharate (having the adult tissues fully-formed within the exuvia).

The presence (X) or absence (—) of stones is indicated, and their weight when measured given to the nearest 0·1 gram.

Crocodiles have been listed in order of habitat, date of capture, and size, and were derived as follows :

Index numbers	Habitat	Date 1956	Captor
1–49	Napoleon Gulf : near Kirinya and Nassau Point	29–31/5	E. Nowotny
50–64	Napoleon Gulf : northern end, near Kirinya and Jinja pier	8–9/6	E. Nowotny
65	Napoleon Gulf : northern end, near Kirinya	16–17/6	D. J. Garrod
66	Napoleon Gulf : southern end, near mouth	1/7	D. J. Garrod
67	Napoleon Gulf : northern end, between Kirinya and Jinja Bay	1/7	D. J. Garrod
68	Albert Nile : Rhino Camp	27/4	African fisherman
69	Lake Victoria : Dagusi Island	17–18/7	African fishermen

Index number	Length (cm.)	Stones (gm.)	Contents of stomach
1	42	—	[M.C. insects.] Terestrial beetle 1. Large grasshopper : *Pseudorhynchus* sp. 1. Spider : *Dolomedes* sp. ♀ (immature ?). Tree frog : *Hyperolius* 2.
2	51	—	[M.C. water-bugs] : *L. fieberi* 1, *Sphaerodema* 1. Tree frog : (*Hyperolius* ?). Nematoda.
3	66	—	[M.C. large earwigs (Forficulina) (5).] Crab : *Potamon* (*niloticus* ?) 1 (*c.* 30 mm.).
4	70	—	[M.C. dragonflies : *I. ferox* f.i. larvae (5)] at least one pharate. Water-bugs : *L. fieberi* 1, *S. grassei* (4). Cricket : (Gryllinae ?) 1. Snail : (*Bellamya* ?) 1. Nematoda.
5	75	X	[E.C. large terrestrial beetle 1.] Nematoda.
6	79	0·3	[M.C. water-bugs : *L. fieberi* (2).] Dragonflies : *I. ferox* f.i. larvae or exuviae (5). Grasshopper (1). Angiosperm material.
7	80	—	[E.C. insects.] Contents lost, but probably water-bugs.
8	82	1·5	[M.C. pellets of short brown fur.] Grasshopper : Acrididae 1. Dragonflies: *T. annulata* wings of immature adults (2). Dead Angiosperm material.
9	84	—	[M.C. insects.] Contents lost, but probably water-bugs.
10	84	—	[M.C. water-bugs] : *H. columbiae* (2), *L. fieberi* (2). Water-beetle : *C. tripunctatus* 1. Anura bones. Nematoda.
11	86	3·9	[M.C. water-bugs : *L. fieberi* (3)], *H. columbiae* (1). Nematoda.
12	87	1·0	[M.C. water-bugs] : *H. columbiae* 1 with eggs, *Sphaerodema* (7) and 1 larva. Cricket : Gryllidae 1. Spider : *Dolomedes* sp. ♀ (immature?) 2. Snail : (*Pila* ?) flesh. Tree frog 1. Nematoda.
13	88	1·2	[M.C. crab : *Potamon* (*niloticus* ?) 1 (*c.* 40 mm.).] Hymenoptera, several. Vertebrate bones (not fish), lost. Green Angiosperm material. Nematoda (alive).
14	89	—	[M.C. insects.] Water-bugs : *H. columbiae* (1) and egg, *S. grassei* 7. Dragonflies : *Z. flavicans* f.i. pharate larva 1, *U. assignata* f.i. larva 1. Spiders : *Trochosa* sp. ♀ 2. Fish : *Haplochromis* sp. 1 (*c.* 40 mm. S.L.). Nematoda.
15	90	1·5	[M.C. dragonflies] : *I. ferox* f.i. (exuviae ?) 3, *Brachythemis* sp. wings (1). Water-bugs : *L. fieberi* 1. Cricket : Gryllidae 1. Snail : flesh and operculum. Angiosperm material.
16	90	—	[M.C. insects.] Water-bugs : *H. columbiae* (1), *S. grassei* (2) and 1 larva. Dragonflies : *A. imperator* mature ♀ 1, *Z. flavicans* (2), *U. edwardsi* f.i. larva with swollen wing-sheaths 1. Tree frog : (*Hyperolius*?) 1.

Index number	Length (cm.)	Stones (gm.)	Contents of stomach
17	19	4·8	[M.C. water-bugs : *H. columbiae* 1 containing eggs], *Sphaerodema* 1. Snail : (*P. ovata*?) flesh.
18	91	7·9	[M.C. frogs : Ranidae] : *Rana* and (*Arthroleptis*?) (8) ; Rhacophoridae : (*Hyperolius*?) 1. Water-bugs : *H. columbiae* (2). Angiosperm leaves (*Trapa*?)
19	93	0·1	[M.C. water-bugs : *H. columbiae* (3).] Spider : *Dolomedes* sp. ♀ 1. Tree frogs : (*Hyperolius*?) 2. Fish : *Tilapia* sp. 1 (*c.* 90 mm. S.L.).
20	93	4·4	[M.C. water-bugs : *H. columbiae* 1 containing eggs], *Sphaerodema* 1. Something lost, perhaps beetle elytron.
21	94	12·7	[M.C. crab : *P. niloticus* 1 (*c.* 55 mm.).] Water-bug (Naucoridae) : *M. flavicollis* 1. Stones : angular quartzite and rounded laterite.
22	94	2·0	Empty.
23	95	3·8	[M.C. fish : *A. nurse* 1 (*c.* 17 cm.).] Water-bugs : *H. columbiae* (3). Dragonflies : *B. leucosticta* f.i. larva 1, *Z. flavicans* mature adult 1. Angiosperm material. Nematoda.
24	95	0·6	[E.C. large terrestrial beetle (*H. colossus*?).] Nematoda.
25	96	0·3	[M.C. tree frogs : *Hyperolius* sp. (4).] Many insects lost, probably water-bugs. Nematoda.
26	96	—	[M.C. insects.] Contents lost, probably water-bugs. Fish remains lost.
27	97	7·2	[E.C. water-bugs] : *H. columbiae* (1), *L. fieberi* (2). Nematoda.
28	98	2·7	[E.C. water-bug : *L. fieberi* 1.]
29	100	18·3	[E.C. water-bugs : *L. fieberi* (2), one with eggs on back.]
30	106	—	[E.C. fish : *T. variabilis* 1 (*c.* 32 cm.).]
31	108	3·4	[M.C. beetle : *H. colossus* 1.] Dragonfly : *Z. flavicans* 1. Other insects lost.
32	108	16·1	[M.C. insects.] Large terrestrial beetle (*H. colossus*?) 1. Water-bugs : *H. columbiae* (2), *L. fieberi* (1). Dragonfly : Gomphidae (*I. ferox*?) f.i. larva 1. Snail : large *P. ovata* mainly flesh 2. Nematoda.
33	110	7·2	[E.C. water-bugs : *H. columbiae* (3), one containing eggs.] Nematoda.
34	110	X	[M.C. fish : *T. esculenta* 1 (*c.* 28 cm.).] Crab : *Potamon* (*niloticus*?) 1 (*c.* 50 mm.). Water-bug : (*H. columbiae*?) 1.
35	115	3·8	[E.C. insects.] Water-bug : *H. columbiae* larva 1 (*c.* 44 mm.). Small cricket (Gryllinae?) 1.

Index number	Length (cm.)	Stones (gm.)	Contents of stomach
36	117	0·7	[E.C. crab : *P. niloticus* mature ♀♀ 2 (both *c.* 50 mm.).]
37	118	35·5	[M.C. bird : feet and culmen of (*G. chloropus*?).] Fine sand.
38	126	13·5	Empty.
39	127	78·0	[E.C. water-bug : *L. fieberi* 1.]
40	130	—	[M.C. crab : *Potamon*] : *P. niloticus* 1 (*c.* 37 mm.), *P.* (*niloticus*?) mature ♀ 1 (*c.* 37 mm.). Dragonfly : *I. ferox* f.i. larva with swollen wing-sheaths 1. Fish : Cichlidae (*Tilapia*?) 1.
41	136	—	[E.C. fish : *Tilapia* sp. 1 (*c.* 25 cm.).]
42	145	23·8	Empty.
43	170	X	[E.C. fish : *T. variabilis* 1 (*c.* 29 cm.).]
44	181	91·8	[E.C. large terrestrial beetle (*H. colossus*?) 1.] Nematoda.
45	197	X	[E.C. fish : *P. aethiopicus* 1 (*c.* 85 cm.).]
46	211	X	[E.C. fish : *P. aethiopicus* 1 (two bone fragments only).] Many stones.
47	272	X	[E.C. fish : *P. aethiopicus* 1 (not longer than 80 cm.).] Dead Angiosperm material.
48	280	X	[E.C. bird : *P. carbo* (large individual) 1.]
49	305	X	[E.C. fishes : *P. aethiopicus* 2 (*c.* 70 and 125 cm.).] Large crocodile hook embedded in stomach wall.
50	57	—	[M.C. water-bugs : *S. grassei* (6).] Terrestrial insect (beetle?) 1.
51	67	1·0	[M.C. water-bugs] : *H. columbiae* (1), *Sphaerodema* (1). Terrestrial insects (Hymenoptera?), several.
52	70	2·4	[M.C. insects.] Water-bug : *Sphaerodema* 1. Dragonfly : Anisoptera : larval mandibles. Hymenoptera, several. Nematoda (alive).
53	72	0·1	[M.C. water-bugs] : *H. columbiae* (1), *L. fieberi* (1), *S. grassei* (6). Dragonfly : Anisoptera : f.i. larva 1. Fish : *Haplochromis* sp. fragments. Nematoda (alive).
54	95	8·8	[E.C. fishes : *Haplochromis* sp. or spp. (2), one *c.* 60 mm.]
55	95	0·9	[E.C. insects.] Water-bug : *L. fieberi* (1). Terrestrial insect (beetle?) 1.
56	102	4·9	[M.C. fish : *M. kannume* 1 (*c.* 48 cm.).] Bird : few black feathers. Dragonfly : *O. trinacria* ♀ probably mature 1. Aquatic Angiosperm stem. Nematoda (alive).
57	105	16·9	[M.C. fishes : small Cichlidae 2.] Dragonfly : *I. ferox* f.i. larva pharate 1. Aquatic Angiosperm leaf (*Vallisneria*?).

Index number	Length (cm.)	Stones (gm.)	Contents of stomach
58	105	11·6	[M.C. Anura (4)] : *Bufo* (*regularis*?) 1, (*Hyperolius*?) 1, frog or toad (2). Water-bug : *H. columbiae* 1. Aquatic Angiosperm leaf.
59	112	2·8	[M.C. toad : *B. regularis* 1.] Dragonfly : *I. ferox* f.i. pharate larva 1. Cockroach : (Blattidae?) 1.
60	115	5·8	[M.C. water-bugs] : *H. columbiae* 2 and eggs, *L. fieberi* (1), *Sphaerodema* 1. Large spider 1. Snail : large *P. ovata* flesh and operculum 1. Nematoda (alive).
61	120	41·0	[M.C. bird : black feathers, filoplumes and rachis of large feather.] Scales *indet.* Water-bug : *H. columbiae* (1). Aquatic Angiosperm leaf.
62	127	42·7	Empty.
63	162	41·8	[M.C. fish : *Tilapia* sp. 1 (*c.* 28 cm.).] Bird : black feathers, some large. Dragonfly : Anisoptera : wings. Beetle (Dynastidae?) 1. Matted roots. Fine sand. Red liquid resembling tomato soup.
64	387	147·8	[E.C. fish : *P. aethiopicus*, well-digested fragments, 1 (*c.* 60 cm.).]
65	115	30·3	[M.C. crab : *Potamon* (*niloticus*?) 1 (*c.* 60 mm.).] Beetle : *H. colossus* 1.
66	65	1·5	[M.C. short brown fur.] Dragonfly : *I. ferox* f.i. exuvia 1, *P. orientalis* f.i. exuvia 1. Terrestrial beetles (4), including *H. rusticus* 1 and *P. spinator* 1. Crab : *Potamon* small (1). Nematoda.
67	98	0·2	[M.C. small Hymenoptera, many.] Large piece of tanned, pared leather.
68	75–90	—	[M.C. insects.] Water-bugs : *S. grassei* 12. Dragonflies : Anisoptera larva (*Urothemis*?) 9, some with swollen wing-sheaths, Zygoptera wing. Hymenoptera, Formicoidea (3) including Camponotinae 1. Prawn : *Caridina* sp. 1. Fishes : *Tilapia* sp. 3 (*c.* 23, 32 and 42 mm.). Cichlidae 1 (*c.* 20 mm.).
69	115	X	[M.C. crabs : *Potamon* (*niloticus*?) (2) (both *c.* 60 mm.).] Fish otoliths (2). Lizard : *V. niloticus* 1 (*c.* 26 cm.). Aquatic Angiosperm material : *Potamogeton* leaf and (*Nymphaea*?) root. Sand.

APPENDIX II

Classification and names of animals listed in Appendix I :

CRUSTACEA	Decapoda-Macrura	Atyidae	*Caridina*
	Decapoda-Brachyura	Potamonidae	*Potamon niloticus* (Milne-Edwards)
INSECTA	Odonata Zygoptera		
	Anisoptera	Gomphidae	*Ictinogomphus ferox* Rambur
			Phyllogomphus orientalis Fraser
		Aeshnidae	*Anax imperator* Leach
		Libellulidae	*Brachythemis leucosticta* (Burm.)
			Orthetrum trinacria Selys
			Trithemis annulata (Beauv.)
			Urothemis assignata Selys
			U. edwardsi Selys
			Zyxomma flavicans (Martin)
	Orthoptera	Acrididae	
		Gryllidae	
		Tettigoniidae	
	Dictyoptera	Blattidae	
	Dermaptera-Forficulina		
	Hemiptera	Belostomatidae	*Hydrocyrius columbiae* Spin.
			Limnogeton fieberi Mayr
			Sphaerodema grassei Poisson
		Naucoridae	*Macrocoris flavicollis* Sign.
	Hymenoptera	Formicidae-Camponotinae	
	Coleoptera	Dytiscidae	*Cybister tripunctatus* Cast.
		Scarabaeidae	*Heliocopris colossus* Bates
		Dynastidae	*Heteronychus rusticus* Klug.
		Cerambycidae	*Phryneta spinator* Fab.
ARACHNIDA		Lycosidae	*Trochosa*
		Pisauridae	*Dolomedes*
MOLLUSCA	Gastropoda	Pilidae	*Pila ovata* (Smith)
		Viviparidae	*Bellamya*
PISCES		Lepidosirenidae	*Protopterus aethiopicus* Heckel
		Mormyridae	*Mormyrus kannume* Forskal
		Characidae	*Alestes nurse* (Rüppell)
		Cichlidae	*Haplochromis*
			Tilapia esculenta Graham
			T. variabilis Boulenger
AMPHIBIA	Anura	Ranidae	*Arthroleptis*
			Rana
		Rhachophoridae	*Hyperolius*
		Bufonidae	*Bufo regularis* Reuss
REPTILIA	Lacertilia	Varanidae	*Varanus niloticus* (L.)
AVES		Phalacrocoracidae	*Phalacrocorax carbo* (L.)
		Rallidae	*Gallinula chloropus* (L.)

STUDIES OF A NUTRITIONAL DISEASE (OSTEODYSTROPHIA FIBROSA) OF YOUNG LIONS ASSOCIATED WITH CHANGES OF THE SKELETON AND SYMPTOMS OF MUSCULAR WEAKNESS

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HISTORY

The existence of a disease of young lions associated with paraplegic symptoms has long been recognised. It is surprising that no references to studies of this disease can be found in the literature although of twenty-two zoos in different countries from which enquiries were made, twelve had experience of it. The aetiology and pathology of the condition does not appear to have been recognised hitherto and it was widely regarded as a myopathy, avitaminosis B or D, or hereditary " rickets ", and views on the measures required to combat it varied considerably.

Theiler (1934 a) recognised that diseases should be classified according to their aetiology. In his (1934 b) paper, he nevertheless applied the term " *osteodystrophia fibrosa* " to a disease of horses of dietary origin and also to von Recklinghausen's disease in Man. Confusion of nomenclature has arisen from this between the group of diseases of the skeleton now known as *osteodystrophia fibrosa cystica*, and which arise from endocrine disturbances, and *osteodystrophia fibrosa* of dietary origin, whose occurrence in young lions is described in this paper.

Theiler (1934 b) has described this disease as it occurs in horses and has given references to the full literature up to that date. The disease appears to have been described first by Germain (1881) amongst horses imported into French Cochin China. It was also recognised in Japan, Ceylon and South Africa but for many years the aetiology remained a mystery. Many workers considered that it was of infectious origin. Ingle (1907) was the first to suggest

that it was associated with mineral constituents of foods and that it might occur where calcium was fed in sufficient quantities but in incorrect balance. Following the work of Ingle, the disease was studied by Sturgess & Crawford (1928) in Ceylon, by Niimi (1927), Niimi & Aoki (1927) and by Niimi & Kato (1927) in Japan ; the same disease was studied by Kintner & Holt (1932) in the Philippines. As a result of this work it was established that the disease was associated with an incorrect calcium/phosphorous balance and might occur although adequate quantities of calcium were, in fact, present. Theiler (1934 b) summed up the position as follows :

> " Reviewing the observations from Japan, Ceylon and Philippines, we see from the data of Niimi and Aoki that the disease can appear very rapidly (five months) even in fairly old animals when the absolute calcium intake is very low (2·1 to 3·6 gm. CaO) and the ratio $CaO:P_2O_5$ [1 to 13] ; from the data of Sturgess and Crawford we see that even when the Ca is adequate (26 gm. CaO) the disease can be produced in healthy young horses in about a year, with a $CaO : P_2O_5$ ratio of 1 : 5, from the data of Kintner and Holt, we see that the critical ratio for arrest or progress of the disease is even narrower, roughly between 1 : 2 and 1 : 3. To be safe, it should be nearer 1 : 1 than 1 : 2."

Since the date of Theiler's paper this disease has been described in horses by many workers in many different countries. Reference to further work in horses is, however, unnecessary ; but it will be advantageous to review such occurrences as can be found in other animals. Reference to it in dogs is omitted because of the possible confusion between *osteodystrophia fibrosa* of dietary origin and that which is well known to occur in dogs secondarily to disease of the kidneys (' renal rickets '). The disease was described in goats by Lesbouyries & Drieux (1951) and by Tajima & Oshima (1951). It was described in pigs by Lesbouyries & Drieux (1951), and by Damoy (1951), and by Liégeois & Dérivaux (1951). In cats it was described by Groulade, Thiery & Drieux (1951), and by Labie, Bourdin & Guillon (1956) ; in these animals it had also been recognised earlier by Baumann (1941) who produced a careful account of a case seen in a kitten. It has been produced experimentally in kittens by Greaves, Scott & Scott (1958). Cordy (1957) described *osteodystrophia fibrosa* in baboons, but he associated the disease with kidney changes which he considered to be secondary to visceral accumulation of lead.

This disease has thus been described in many parts of the world and in a wide variety of animals. The confusion between the glandular form of *osteodystrophia fibrosa* and the dietary form is unfortunate. There should, however, be no difficulty in distinguishing clinically the one from the other. The disease which arises from dietary causes does not show the bony distortion associated with glandular disease, nor the replacement of mineral in the bones by osteoid material which gives rise to the " rubber bones " syndrome.

In lions, the existence of a paraplegic disease has been known for many years. There appears to be a reference to it in Sterndale's (1884) " Mammalia of India ". The disease does not hitherto appear to have been associated with changes of the skeleton and its essential nature has thus remained unrecognised.

TABLE 1

Showing incidence of the disease noted by other zoological collections.

Name	Recognition of symptoms	Diagnostic observations	Age	Any other observations and treament
Bristol, Clifton & West of England Zoological Society	Yes	Vitamin B deficiency	cubs	Cured by 'Marmite'.
Dudley Zoological Society Ltd.	Yes	Vitamin B deficiency and diet	6–12 months	Also leopard. B complex and whole animal as diet.
North of England Zoological Society, Chester	Yes	Interbreeding, trauma	young	
Paignton Zoological and Botanical Gardens, Ltd.	No	—	—	—
Zoological Society of Glasgow and West of Scotland	No	—	—	—
Royal Zoological Society of Ireland (Dublin)	No	—	—	—
Royal Zoological Society of Scotland	Yes	Heredity	young	Adult male outgrew symptoms. All his litter mates affected.
Cleveland Zoological Society				
Detroit Zoo	No	—	—	—
New York Zoological Society	Yes	Rickets	young	Feed bone meal
Philadelphia Zoological Gardens	Yes	Rickets and/or deficiency	young	A, D and B complex
St. Louis Zoo	Yes	Digestive	young	Not seen in tigers
San Diego Zoo	No	—	—	—
Seattle Zoo	Yes	CNS, nutrition	young	Also in other cats. Vitamin D increase in protein
Washington Zoo	No	—	—	—
Amsterdam Zoo	No	—	—	—
Bellevue Zoological Gardens, Belfast	No	—	—	—
Copenhagen Zoo	No	—	—	—
Moscow Zoopark	Yes	Post infectious	young	Only seen as a complication
Rotterdam Zoo	Yes	Diet	young	'Stargazers'. Fed frequently on whole guts. Inbreeding.
Tokyo Zoo	Yes	Rickets	young	Diet fortified with whole rabbit
Imperial Veterinary Laboratory, Addis Ababa	Yes	—	—	Similar to Imperial lions in Addis Ababa
Game Department, South Africa	Yes	Meat diet	Two years	Noted in circus lions—appetite normal, fat

Spinal cords were examined at Bristol in recent years in an attempt to ascertain the cause of the trouble ; the Superintendent, Bristol Zoo in a private communication to one of us (O.G-J., 1959) said that Laidlaw & Dunkin had reported that the nervous system showed no evidence that any virus infection could be involved and that Mellanby, as a result of examination of spinal cords, considered that deficiency of vitamin B_1 was the cause.

Table 1 shows the results of enquiries made from a number of British and foreign zoos. From these it appears that the condition is widely known, but the cause not understood. It is not mentioned by Fox (1923).

CLINICAL HISTORY

Amongst a total of thirty-two lions exhibited at Regent's Park over the past seven years, eight have shown signs of the disease described, and have been observed clinically by one of us (O.G-J). Of these, four have died or have been destroyed and three (possibly four) still survive. Of the survivors two are at the present time (1959) on exhibition in the Regent's Park gardens. The animals that survived suffered from recurrent attacks of the symptoms and treatment consisting of B group vitamins and additional mineral salts in the form of a mineral mix was given. It has also always been the practice in recent years at the Zoological Gardens to feed to lions the whole carcass of rabbit, chicken, pigeon, and even goat when possible. The affected animals have thus evidently been subject to alternating periods when their mineral balance has approached what is desirable and other when the balances, as will be seen, have been outside the range necessary for the maintenance of health.

The clinical notes are derived from a study of these eight animals and in particular of two, " Alberta " and " Calgary ", which have been under intensive study for more than two years. The following is a general description of the disease as observed :

Age : The animals affected are usually between twelve months and two years, and consequently, still growing and adolescent.

Sex : There seems to be no specific susceptibility of either sex.

Occurrence : The disease has been seen in imported and home-bred animals, but there is no information that it has ever been seen in the wild.

General symptoms : An affected animal shows no apparent skeletal deformities but is affected by a progressive inability properly to co-ordinate voluntary movement of skeletal muscles. Initially, a weakness of the hind legs is noted in an otherwise normal animal, typified by the legs sliding away from under the animal on a sharp turn. Progressively over the weeks, the forelegs become affected and there is a degree of muscle wastage noted on the fore and hind quarters which may produce an exaggerated display of the dorsal aspect of scapula movement during walking. All sphincters remain in normal function and appetite and digestion are unimpaired. The nature of the animal can change from placidity to an aggressive nervousness with part hyperaesthesia. Thus tactile responses seem to vary from normal to exaggerated while other

reflexes such as those of sight and hearing remain normal. The posture of the ears when quiescent is usually less alert. Two lionesses (" Amber " and " Asha ") exhibited a strange symptom which can only be described as a dance. During this " dance " the hind legs would remain stationary, while the fore legs were alternatively picked up, as in " marching on the spot ". The head simultaneously would be tossed about. This would go on for as long as a minute at a time. As mobility becomes progressively affected, the tail is used more and more as a stabilizer to counteract postural weakness. The position of the head varies from normal to lateral deviation with rotation to left or right. Occasionally " stargazing " is observed, coupled with a moronic expression. The visible mucous membranes appear pink and healthy but it has not been possible to record body temperatures.

The untreated disease can run either an acute or a chronic course.

(a) The acute case will progress from incidence to death in about twelve weeks. Death usually occurs from inanition with a superimposed secondary cause such as pneumonia.

(b) The chronic case will vary in intensity for several weeks but will recover within six months to apparent normality, though regressive attacks are seen. In some of the chronic cases which recover once maturity is reached it seems that the animal will remain well. As is the case in the acute syndrome, some chronic cases are overtaken by secondary diseases, perhaps due to lowered resistance. The part played by virus disease, such as panleukopenia (infectious feline gastro-enteritis) is not clear, but in all the cases seen in Regent's Park there is no clinical history of such disease occurring. All the animals noted as having been affected had been vaccinated against panleukopenia with egg adapted virus vaccine. If panleukopenia has been present, it must have existed as a sub-clinical entity displaying no symptoms, and if this is the case, it is arguable whether CNS damage had occurred as a pre-disposing factor.

A clinical examination of the affected lion " Calgary " and the lioness " Alberta " was made by Dr Dennis Williams of the National Hospitals for Nervous Diseases, Queen Square, London, W.C.1. Dr Williams reported as follows :

> " When I saw the lions the following facts emerged from observation : when walking they had a very ataxic gait with obvious weakness of muscles of both sides of the body equally, and apparently of all four limbs equally. The weakness seemed to be most marked in the peripheral muscles and they had foot drop in all their feet. The ataxic gait was a flaccid one and there was nothing at all on observation to suggest spasticity. The beasts were sufficiently weak for them to fall over when making sideways movements because their hip and shoulder fixing muscles were not strong enough to hold their weight. In contrast to this, there was no evident weakness of the muscles of the face, neck or trunk and respiration was certainly not embarrassed. I gather though that in another animal that has been seen there was weakness of back muscles also. This is probably just a question of degree because it is quite common for weakness which begins peripherally to become proximal in more severe cases as for instance in acute infective polyneuritis

in Man. When they were walking it did not seem that the beasts had any discomfort, suggesting that there was no distortion of sensation in the pads of their feet. Equally they did not at any time seem to be in physical distress.

" Sitting, the lions looked normal, and it is important that there was no abnormal posture of the head ; eye movements were full, pupils were normal, they reacted to light and there was no squinting. Facial movements were normal. I gather that they chew satisfactorily and they swallow normally. We can take it, therefore, that there is no significant involvement of any cranial nerves, and that the cerebellar and vestibular mechanisms are intact.

" They are stated to have normal control of bladder and bowels.

" The next point was to decide whether the flaccid ataxia was due to sensory loss or not, and we were able to demonstrate very convincingly that the appreciation of pin prick and of light touch and pressure was normal on the dorsum of both fore limbs. Equally there was reflex withdrawal on light touch of the hairs. We can conclude with absolute certainty, therefore, that there is either no sensory loss at all or not enough sensory loss to account for the animals' disability.

" It is known, therefore, that this condition is the result of diffuse symmetrical and mainly peripheral muscular weakness. It can be taken as a reasonably certain fact that there is no clinical evidence of involvement of the central nervous system, and that the whole condition is either in the peripheral nerves or in the muscles ".

Lioness " Alberta " was also examined by Dr A. T. Richardson, Dr C. Symons and Dr C. B. Wynn-Parry of the Royal Free Hospital, Hampstead, who made electromyograms and electrocardiograms. Their report on this case is as follows : —

" The lesion appears to be one producing lower motor neurone degeneration and, therefore, comparable to polyneuritis of human adults. This is based on the fact that intensity (strength) duration curves taken from the left forelimb were typical of partial denervation. Electromyograms taken from that limb and the left hindlimb showed fibrillation potentials at rest and on volition a mixture of motor unit potentials, some of which were comparable with a duration in the order of 5 m. secs. and an amplitude of 500 micro-volts and some of which were of much longer duration (10–12 m. secs.) and comparable to the type of motor unit potentials found in recovering polyneuritis in humans ".

Dr Symons reported that an electrocardiogram made at this same time showed no features which could be considered abnormal.

Some comprehensive blood chemical analyses made by Dr D. Baron of the Royal Free Hospital, Hampstead, gave inconclusive results which may, in part, be due to a lack of knowledge concerning the normal blood chemistry of lions. In horses, however, blood chemical studies have not been found of value

for diagnosis. Kintner & Holt (1932) made extensive blood chemical examinations in affected and normal horses and found that the blood calcium was slightly reduced and the inorganic phosphorus slightly raised. Groenwald (1937) reported blood calcium findings to be of no diagnostic value. Baron's results are given in Table 2.

TABLE 2

Blood examination, 'Alberta', by Dr Denis Baron.

Serum total proteins :	7·1 g./100 ml.
albumin :	4·0 ,,
globulin :	3·1 ,,
γ-globulin :	1·7 ,,
Van den Bergh. direct :	negative
total bilirubin :	0·5 mg./100 ml.
alkaline phosphatase :	2·3 ,,
thymol turbidity :	negative
thymol flocculation :	negative
colloidal gold :	negative
Blood Urea	51 mg./100 ml.
Serum potassium :	6·0 mEq./l
sodium :	167 ,,
chloride :	116 ,,
Serum amylase :	8,000 units/100 ml. (Somogyi)
Serum transaminase :	6 units
creatine :	0·7 mg./100 ml.
creatinine :	2·0 ,,
Spectroscopy : No abnormal pigments detected	
Serum uric acid :	1·1 mg./100 ml.
Serum calcium :	10·8 mg./100 ml.
inorganic phosphorus :	7·6 mg./100 ml.
magnesium :	1·95 ,,
amino acids :	16 ,,
cholesterol :	105 ,,
lipase :	0 units

Serum Amino-acid Chromatography

50 μl. ultrafiltered, desalted serum run both oxidised and 'plain'.
Glycine, taurine, glutamic acid, alanine, glutamine—present in heavy concentration. Serine, valine, leucine present in moderate concentration. Trace of aspartic acid present. Oxidation did not reveal presence of cystine or methionine.
Larger amounts of ultrafiltrate 'overloaded' chromatogram. Amino-acids mentioned present in considerably greater concentration than in man.

Serum Indole Chromatography

0·5 ml. ultrafiltered, desalted serum run. Urea spot and trace of tryptophan only

DIETETIC FACTORS

Tables 3 and 4 give an analysis of the food given at Regent's Park to the resident lions over a period of one month. This may be taken as typical of that which has been given over the past few years. Table 4 shows the percentages of meat and bone which were eaten. The meat given is a second grade meat from the abattoir which has been passed fit for human consumption. There is thus no question but that the quality and quantity have been good. Indeed, many adult lions appear to obtain their nutritive requirements from this diet and have shown no apparent symptoms.

TABLE 3

Showing quantities of meat and bone given to seventeen lions and other large felines of different ages recently at Regent's Park.

Figures are four-weekly averages, weight in lbs.

Name	Amounts given		Amounts removed		Amounts retained	
	Meat	Bone	Meat	Bone	Meat	Bone
LION						
'Pampas'	42	24	1	19	41	5
'Judy'	39	22	3	20	36	2
'Rex'	44	24	4	22	40	2
'Elizabeth'	42	23	4	21	38	1
'Rusty'	42	21	5	19	37	2
'Amber'	39	23	6	21	33	2
'Sultan'	46	23	9	21	35	2
'Lyle'	37	22	0	16	37	6
'Bewildered'	39	24	6	22	33	2
'Janet'	38	25	4	24	34	1
TIGER						
'Nefti'	46	24	6	20	46	4
'Mistress'	47	22	0	19	47	3
'Susie'	39	24	2	21	37	3
'Rose'	33	21	4	19	29	2
'Nassau'	32	21	1	19	31	2
JAGUAR						
'Jill'	21	15	0	10	21	5
PUMA						
'Thomas'	20	12	1	11	19	1

N.B.—Apart from the bone, the dietaries consisted of mainly beef with some horse. A little venison was given when available, and one week of the four rabbit, liver and pigeon, was added. An additive of bone flour and cod liver oil was also given.

This diet has a low Ca/P ratio. That of uncooked meat is approximately 1 : 20, whereas in most animals, including cats (*vide* Scott, Scott & Greaves, 1958) the ratio should be in the region of 1 : 1, and in horses, at any rate, a wider ratio than 1 : 4 would be expected to initiate *osteodystrophia fibrosa*.

The very wide ratio of whole red meat is, of course, corrected to a certain extent by the small amount of bone that is eaten, and by any bone flour provided, and this, with other additives, appears to enable the adult animals to survive without exhibiting any symptoms of dietetic imbalance.

One severely affected lioness, " Anne ", following treatment over some six to seven months, made great progress and was discharged from the Hospital. This lioness was given calcium gluconate in her water and her meat was fortified with calcium carbonate. The estimated daily intake of calcium gluconate was six ounces.

TABLE 4

Percentages of meat and bone eaten over a period of one month. Weights in lbs.

Name	Total meat	Total bone	Meat Percentage	Bone Percentage
Lion ' Pampas '	162¼	18	90	10
Lioness ' Judy '	146½	9	94·2	5·8
Lion ' Rex '	158	7½	95·7	4·3
Lioness ' Elizabeth '	151¾	2½	98·0	2·0
Lion ' Rusty '	149	8½	94·9	5·1
Lioness ' Amber '	135¼	3	97·8	2·2
Lion ' Sultan '	146½	6½	95·4	4·6
Lion ' Lyle '	147¾	20½	88	12
Lion ' Bewildered '	129¼	4½	96·2	3·8
Lioness ' Janet '	137½	5	96·3	3·6
Tigress ' Nefti '	184½	14½	92·4	7·6
Tigress ' Mistress '	187¾	13½	93·5	6·5
Tigress ' Susie '	149	7¾	93·9	5·1
Tigress ' Rose '	113½	6½	94·3	5·7
Tiger ' Nassau '	120¾	6¾	94·4	5·6
Jaguar ' Jill '	82¾	10½	89·2	10·8
Puma ' Thomas '	78½	4½	93·9	6·7

PATHOLOGICAL STUDIES

Pathological studies were made on two young lions ' Alberta ' and ' Calgary '. The following is an account of what was found.

General

The two lions affected were twins, ' Calgary ' being the male and ' Alberta ' the female, that had been presented by the Mayor of Toronto to the Lord Mayor of London and deposited at the London Zoo, where they were received on 26. 10. 55 and remained for nineteen months and twenty-three months respectively. Since they were about six months old on arrival, their ages were twenty-five months and twenty-nine months at the time of death.

They had appeared healthy on arrival in England but the paraplegic symptoms had developed progressively and the disease did not respond to treatment. When ' Calgary ' was twenty-five months old he developed a mild respiratory complaint from which, owing to his condition, he collapsed and was, therefore, painlessly put to death by means of barbiturate injections. as was ' Alberta ' four months later.

General Condition

There was evident wasting of the muscles of both fore and hind quarters. Otherwise both lions were in very good condition, appeared well nourished, and coat and skin were loose and healthy. There was abundant fat of a bright, healthy colour and normal consistency. The subcutaneous tissues appeared quite normal. There was no excess fluid in the abdominal or thoracic cavities.

The Musculature

In both lions the general musculature of limbs and body was abnormally pale. This remark applies equally to both flexor and extensor groups. The muscles of the face and jaw, however, were normal in appearance.

Portions of various muscles from ' Alberta ' were examined at the School of Tropical Medicine by Dr Yei for 'trichinosis ' with negative results.

Portions of muscle from ' Calgary ' were examined histologically by Dr Mair at the National Hospital for Nervous Diseases, Queen Square. He reported on them as follows :—

> " Portions of the *biceps muscle* showed occasional atrophied fibres with numerous nuclei. These atrophied fibres had lost their striations. In parts of the muscle there were collections of small round cells. This change is not typical of that seen in denervated muscle.
>
> " Portions of the *deltoid*, *vastus medialis*, *latissimus dorsi* and *gracilis* were also examined but significant changes were not seen."

Dr Mair also showed sections to Professor Wolfahrt from Lund, an acknowledge expert in myology. He stated that the slight muscular changes were non-specific.

Specimens of muscles from ' Alberta ' were aso examined by Dr J. N. Walton of the Royal Victoria Infirmary, Newcastle-upon-Tyne. Dr Walton commented as follows :—

"The sections of muscle are, in my opinion, normal. Areas of hyaline necrosis are non-specific fixation artefacts, such as are commonly seen in human muscles. This is evident because there is absolutely no cellular reaction to this necrosis and if it had been due to a myopathic disorder then without doubt there would have been some evidence of phagocytosis of necrotic sarcoplasm. In fact the muscle fibres are uniform in shape and size, there is no enlargement of sarcolemmal nuclei and I can find nothing to suggest either a myopathy or neuropathy."

The Alimentary Canal

In both lions numerous nematodes (*Belascaris* sp.) were present in the duodenum. In the case of 'Calgary', histological examination showed eggs and larvae of this worm to be embedded in the mucous membrane at the base of the villi. In this site the worms were obviously responsible for causing mechanical damage.

In both lions the small intestine appeared to be much thickened. The mucous membrane did not strip readily but was very hyperaemic and rose red in colour. In 'Calgary' the hyperaemia was more pronounced dorsally; in 'Alberta' it was uniformly distributed. This condition of the small gut may well have been associated with the presence of the worms and have had no association with the condition being studied. On the other hand it will be necessary to determine whether the presence of the worms or of migrating worm larvae could be associated with the main condition.

Histologically hyperaemia was marked and there was desquamation of the superificial layers of the mucosa.

The Liver

In both lions the liver showed peculiarities which are worthy of note. There were differences between the two sides of the same organ. The left side, which receives the bulk of its blood from the spleen, was pale in colour, normal in size and firm in texture. The right side was swollen, dark in colour, very congested and soft. On histological examination, the left side was normal; the right was congested and many cells contained droplets of fat.

This difference is of interest, since the spleens in both lions were swollen and congested, and yet the portion of liver receiving portal blood from this source was normal; the congestion was on the other side. This state of the liver is not necessarily abnormal since something similar has been noted in tigers.

No abnormalities were seen in the gall bladders.

The Pancreas

In both lions the pancreas was normal both macroscopically and microscopically.

The Spleen

In both lions the spleens were greatly engorged with blood and appeared dark in colour, tumefied and mottled. There were no pathological changes, the state of the organ being due to haemostasis or hyperaemia.

The Endocrine Glands

In both lions the pituitary gland was small and the *pars distalis* consisted chiefly of basophilic tissue. There did not appear to be any definite abnormality, and the *sella turcica* in the lion also is so small as to suggest that the pituitary cannot be a large structure.

In both, the thyroids were much enlarged and histologically the acini showed great variations in size. They were full of colloid and many were abnormally large. It is difficult to assess these changes, because no normal lion thyroid is available for comparison. Nevertheless, the organs appeared to be hyperplastic and resembled the condition of the thyroid, which is associated with iodine deficiency.

In the case of 'Calgary' both adrenals were haemorrhagic, small and unpigmented. Those of 'Alberta' were unfortunately mislaid.

The Respiratory System

Nothing abnormal was found in the lungs or other respiratory organs of 'Alberta'. 'Calgary', as already mentioned, had developed respiratory symptoms which resulted in his collapse. The lungs were pale and shrunken with superficial areas of emphysema ; the intermediate lobes of the left lung showed almost complete atalectasis. Throughout the lungs there was mild peribronchitis, but without any extensive areas of consolidation.

The Circulatory System

The heart and blood vessels of 'Alberta' were normal. In the case of 'Calgary', the heart was normal but longitudinal roughening was found at the beginning of the aorta. The following description of the histological picture was given by Dr H. E. D. Lloyd of the Bland-Sutton Institute of Pathology :—

> "The whole aorta appears thickened. The media shows mild elastic tissue degeneration and mucoid accumulation.
>
> "The vasa vasorum are thick-walled. The adventitial vessels are surrounded by chronic inflammatory cells ; this applies also but to a lesser extent to the vessels in the media. The intima appears normal.
>
> "It is difficult to believe that these changes could ever be considered normal in a three-year old lion. There is no evidence of active inflammation."

It seems very doubtful if these changes could be associated with the condition under study. They would appear to be post-inflammatory.

The Lymphatic System

In both lions the mesenteric and renal glands were much enlarged and oedematous. The other lymphatic glands of the body showed no abnormalities.

In sections of the lymphatic glands outstanding changes were not seen. The lymph channels were open and there were few cells to be seen in them. The lymph nodes were normal in appearance, though cells were inclined to be scanty. One or two lymph nodes tended to show ' Flemming's Centres '. The medulla was remarkable in showing a dearth of both lymphocytes and blood cells. The cells of the reticulum appeared to be fine and stretched.

The general picture is one of enlargement of the gland, accompanied by some depletion of lymphocytes. The histological picture thus supports the macroscopic appearance of odema.

The Urinary System

There were no abnormalities seen in any part of this system.

The Reproductive System

In the case of ' Alberta ' no abnormalities were seen. In the case of ' Calgary ' the testes were small, only partially descended, and appeared under-developed. The epididymides and prostate were large.

The Nervous System

In neither lion were any significant changes found in the peripheral nerves. Careful examination of the spinal cord in ' Alberta ' failed to reveal the presence of helminth larvae in any portion and none were found in the case of ' Calgary '. This search was made because of the presence of so many *Belascaris* in the duodenum, which gave rise to the suspicion that migrating worm larvae might be the cause of the condition.

In both lions there were mild demyelinating lesions chiefly in the ventral portion of the cord and in the cerebellar peduncles and adjacent areas of the cerebellum. In the case of ' Calgary ' the entire cord and brain were taken to the National Hospital, Queen Square, for examination. For the following account of the condition of this cord we are indebted to Dr Marion Smith :—

" In each segment examined the degeneration affects both sides of the cord, in identical location and extent.

" The appearance of the degenerating fibres suggests that the degeneration is of fairly recent origin." (This opinion is of interest in comparison with inferences from the condition of the skeleton, which suggest that the onset of the skeletal changes occurred at an early age, i.e. when ossification was not far advanced ; it is possible that the nervous changes may have an independent origin or be sequelae of the primary condition.)

" *Cervical Segment.* In the dorsal columns there is considerable degeneration in the most lateral fibres of the *fasciculus gracilis*, and less extensive degeneration in the most medial part of the *fasciculus cuneatus*.

"In the lateral and ventral columns there is considerable bilateral degeneration of fibres in the peripheral field, including the ventro-medial zone bordering the medial fissure. The degeneration is most marked in what appears to be the dorsal and ventral spino-cerebellar tracts, esp. in the dorsal tract. There is a little scattered degeneration in the more medial fibres of the columns.

"There are some degenerating fibres in the ventral horns, esp. in the most ventral part.

"*Thoracic Segment.* In the dorsal columns there is degeneration scattered through a fairly wide zone, with degeneration free regions medial and lateral to it. There is no degeneration in the entering roots at this level.

"In the lateral and ventral columns there is widespread degeneration, which is most marked in the most lateral part of the dorso-medial region. There is less degeneration in the dorso-lateral region than elsewhere in the columns and, on the whole, the degeneration is less abundant in the peripheral field than in the more medial region.

"There are a few degenerating fibres in the ventral horns.

"*Lumbar Segments.* In the dorsal columns there is no degeneration with the possible exception of a very few fibres.

"In the lateral and medial columns the degeneration is most abundant in the ventral part of the dorso-lateral and dorso-medial region and in the more medial fibres of the dorsal part of the dorso-lateral region.

"There are a few degenerating fibres in the ventral horns.

"*Conclusions.* Too few segments have been examined to permit any final conclusions. The appearances described would suggest a fairly diffuse lesion in the lower thoracic cord affecting most of the lateral and ventral columns, and two or more dorsal roots. The distribution of the degeneration in the cervical and lumbar segments is in keeping with the pattern of degeneration in ascending and descending tracts respectively."

No guess is hazarded as to a possible cause of such a lesion, which is what we are trying to establish. It may, however, be said that the appearances in the cord and brain do not suggest an inflammatory origin of the trouble. Indeed, the absence of cellular reactions and perivascular cuffing would appear to negative any idea that this condition may be the sequel of a virus infection such as cat distemper. This was a possibility that was at one time seriously considered.

The Skeletal System

Severe changes of the skeletal system were present in both lions and the following is a composite account derived from conditions found in both:—

The Teeth. The teeth were well formed, white and bright, with normal appearing enamel coat. The canines, however, were very light in weight, and the dentine very thin. The pulp cavities were greatly enlarged, accounting for the lightness and the thinness of the dentine. In spite of the well-formed appearance, the teeth were hollow, instead of solid, structures.

The Mandibles. These bones showed severe osteo-porosis, esp. towards the anterior ends of the rami and in the tooth sockets. The articular surfaces also were rough and porotic.

The Nasal Bones. The sutures between the nasal bones were not united, and the bones appeared to be somewhat shortened. Both bones were very rough and porotic.

The Ethmoid. In ' Calgary ' the nasal septum had never completely ossified anteriorly. The posterior ossified portion was distorted due to downward pressure during the ossification process. The circumstance can be used to date the onset of the disease, at a time when the bone was incompletely ossified.

The Turbinates. All the turbinates of ' Calgary ' showed a measure of ' pressure' distortion. The bones on the right were considerably smaller than those of the left.

The Maxillae and Premaxillae. These were amongst the bones to be most severely affected. Osteoporosis was particularly severe in the region of the tooth cavities. There were signs of periodontal haemorrhage.

Basi-occipitals and Basi-sphenoids. The sutures between these bones were not firmly united. This is possibly not abnormal.

Temporal Bones. The wings of the temporal bones forming the zygomatic arch were very rough and porotic.

Occipital. On the body of this bone the spongy bone was increased at the expense of the compact.

The Frontals. These bones were very thick, compact and dense in contrast to the other bones of the cranium. The sutures were firmly united.

The Zygomatics. The whole zygomatic arch showed severe osteo-porosis.

At the time of post mortem on ' Calgary ' the usual practice was followed and the limb bones were not retained. When ' Alberta ' was autopsied it had become clear that it was also necessary to study the condition of these bones, to which the following description refers.

The Scapulae. The weight of the scapula of the right fore limb exceeded that of the left by 19 grammes. That of the right side was composed of compact, dense bone and showed no changes that might be associated with disease. The bone from the left limb was light and the flat portion was very thin. The bone showed marked hyperaemia. There was severe osteo-porosis affecting the distal end of the bone. In particular, the articular surface was seriously affected and both the interior and exterior surface of the articular rim showed exostoses.

The Humerus. An osteo-porotic condition is present at the proximal ends of both these bones. Here compact bone is deficient, while distally the compact bone is thick and strong. The right humerus is denser and heavier than the left and shows no deformity. The left humerus shows mild exostosis on the left articular rim. This bone is very hyperaemic.

Radius and Ulna. The radius and ulna of the right side are considerably heavier and denser than on the left ; the right radius exceeds the left in weight by 28 grammes and the right ulna exceeds the left in weight by 42 grammes. The bones of both sides tend to be hyperaemic. On neither side is there any marked deformity.

The Pelvis. The right-hand pelvic bone is slightly heavier and denser than the left. On the right there is a coarse osteo-porotic condition towards the posterior edge of the sacro-iliac articular surface. Apart from this the bone appears strong and well formed. The left hand bone shows a fine osteo-porosis with loss of compact bone on the under surface of the ischium ; this is most severe in the region of the symphysis and anteriorly.

The Femur. There appears to be little difference in condition, including weight and compactness, between the two femurs. Both proximally and distally the compact bone is deficient and there is a severe osteo-porotic condition.

It may here be mentioned that in these bones, as in all the long bones and some flat bones, e.g. scapula, epiphyses and diaphyses had not united. The distal ends of the tibias were the only exceptions to this.

The Tibia. There is no significant difference in weight between the two tibias, and the condition of the two bones appears to be roughly equal. The central areas of the shafts appear to be normal, but—as in the case of the femurs—the proximal and distal ends of both bones are diseased. The compact bone is deficient and there is both coarse and fine pitting, which extends to some extent over the distal articular areas. Distally the bone on the right side appears to be more severely affected.

Fibulae. The fibulae both show considerable pitting in the proximal and distal portions.

It would have been interesting to examine the bones of the vertebral column. Unfortunately, however, this was destroyed during removal of the spinal cord.

General. The general lesion of the skeletal system is typical of that of *osteodystrophia fibrosa* of dietary origin as seen and described in horses and other animals. This lesion is characteristic and easily distinguished from the *osteodystrophia fibrosa cystica* of von Recklinghausen's disease associated with parathyroid tumour or with the " renal rickets " syndrome. *Osteodystrophia fibrosa cystica* is associated with gross distortions of the skeletal system together with increased osteoid tissue in the bones, that is tissue formed of bone protein and with the cystic condition from which its name is derived. *Osteodystrophia fibrosa* of dietary origin is associated with little actual deformity of the skeleton and it is for this reason that the essential nature of the disease as being one associated with the skeleton is less easily recognised. The bones and teeth become light because of removal of mineral salts from their substance but the essential architecture is unchanged. Thus the naturally occurring haversian systems and canaliculi of the bones are of normal structure but the lacunae are increased in extent. The compact bone becomes thinner and the spongy

bone more extensive. In the case of the teeth the pulp cavity becomes much enlarged, although to outward appearances the teeth are normal.

The disease as seen in young lions does not appear to be progressive but subject to intermission at times when perhaps calcium salts are available by additions of whole carcass to the diet as described. It thus appears that from time to time compact bone may be laid down and subsequently more mineral salts may be removed. This may account in part for the differences in the bones of the two sides of the body.

These differences may also in part be attributed to the habit of affected lions of lying chiefly on one side thus possibly causing differences in the distribution of the blood between one side and the other.

The Blood

Physical examination of the blood of ' Calgary ' was made. This showed that the blood picture was normal in every respect. Figures for red cell count, haemoglobin and packed cell volume were, if anything, higher than would be expected.

The peculiar tendency to hyperaemia in many organs will have been noted and this appears to be a feature of the disease. We have encountered this in the small intestine, the spleen, the right side of the liver, and now finally and most characteristically in the diseased bones.

DISCUSSION

There appears little doubt that the disease described is primarily one affecting the skeleton. If this is agreed, then the diagnosis of *osteodystrophia fibrosa* of dietary origin must follow from the nature of the bony lesions. Confirmatory evidence comes from two sources :—firstly, the successful attempt to treat lioness ' Anne ' by added calcium in the diet, secondly, from the studies of Greaves, Scott & Scott (1958), who experimentally produced a very similar disease in young cats by feeding them on a sole diet of ox heart and tap water. Secondary to the changes of the skeletal system have been apparent changes of the muscular system and actual changes in the nervous system. The changes in the muscular system, as is now known, were secondary to those of the nervous system. It is possible, of course, that the lesions of the nervous system are caused by some similar but different factor. Nevertheless, nervous changes may well accompany disease of the skeleton without the intervention of separate aetiological factors (*vide* Mitchell, 1935 a, b).

SUMMARY

1. Studies have been made of a disease of young lions in captivity which has been a source of difficulty in many zoos and other places.

2. These studies have embraced the symptoms and course of the disease, the clinical and pathological symptoms, the morbid anatomy and the biochemistry.

3. This disease had hitherto, owing to the outward signs, been ascribed to a variety of causes including myopathy and various vitamin and other dietary deficiencies.

4. The studies have shown that a number of the bodily systems suffer derangement or damage during the course of the disease, and a number of possible causes required to be eliminated. Thus apparent changes occur in the skeletal system, the nervous system, the alimentary system, and the endocrine system. In addition there was the possibility that the disease might be associated with helminthiasis or with the effects of post-viral infection.

5. It has been demonstrated that the primary lesion is that of the skeleton and that this is an *osteodystrophia fibrosa* resembling the well-known condition described by Theiler and others.

6. The disease appears to be associated with an unnaturally low Ca/P ratio in the diet normally fed to captive lions which consists mainly of red meat. It has not been widely recognised that the Ca/P ratio of red meat is about 1 : 20 and that lions consume bones only sparingly and thus do not tend to correct this wide ratio.

7. Once established, skeletal deformities tend to subsist and complete cure in the sense of a return to normal cannot be effected by correction of the dietary ratio. Great improvement has, however, been effected in the case of one lioness who was given calcium supplements and improved to such an extent that she was able to go back on exhibition in the Zoological Gardens. Two other young lions, sent from Whipsnade Zoo for treatment, were subsequently cured by similar means.

ACKNOWLEDGMENTS

The extent to which the authors have benefitted by specialist assistance and advice will be evident from the text, and to all those persons who have helped we extend our grateful thanks. In addition, we would like to add our thanks to Dr Patricia Scott of the Royal Free Hospital, Gray's Inn Road, to whom we are greatly indebted. Dr Scott's experience over a similar condition in the domestic cat was invaluable to us at a crucial moment in our own work.

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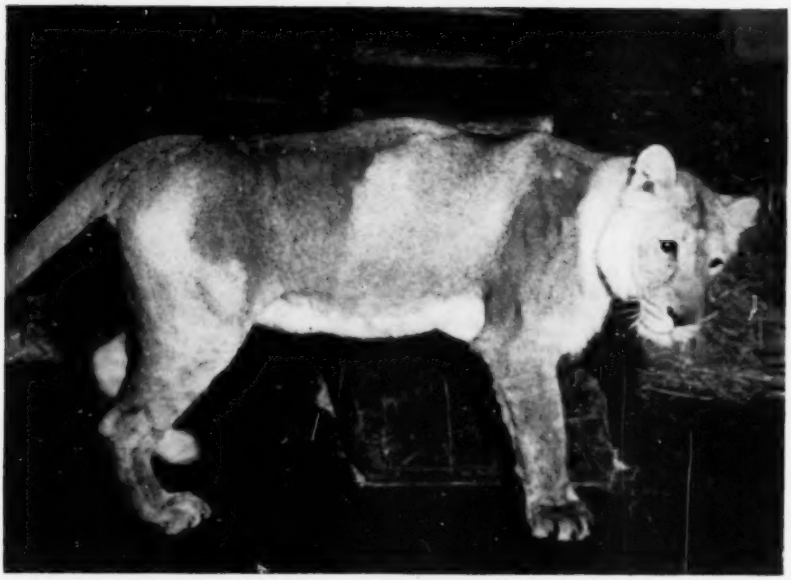

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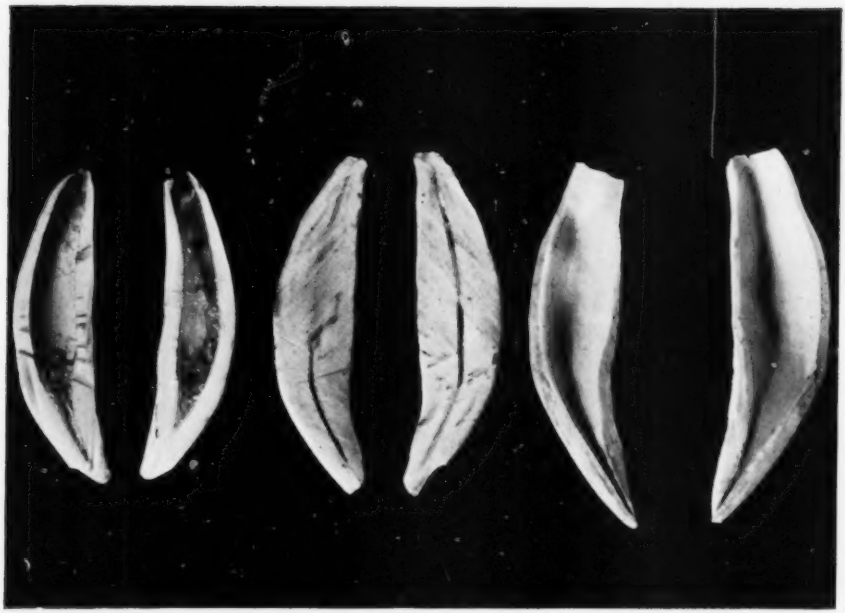

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Fig. 1.—Lioness "Asha"—acutely affected with osteodystrophic disease.
Fig. 2.—Canine teeth sectioned to show condition. The central tooth is normal. To left and right those of "Alberta" and "Calgary".

1

2

Fig. 1.—Mandible of "Calgary" showing the osteoporotic condition of the bone.
Fig. 2.—Right and left scapulae of "Alberta" showing the dissimilarity between the two sides.

1

2

Fig. 1.—Right and left tibia of "Alberta" showing dissimilarity of the two sides and osteoporotic condition of the bone.

Fig. 2.—Ulnas of "Alberta" showing the same dissimilarity of the two sides and osteoporotic condition

TUBERCULOSIS OF A PUMA CUB (*FELIS CONCOLOR*) ACCOMPANIED BY SKELETAL DEFORMITIES RESEMBLING RICKETS

BY

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Zoological Society of London

[Accepted 10th February 1959]

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CLINICAL HISTORY

A young female puma cub was born at Whipsnade on 26. 11. 57. The animal was kept at Whipsnade in open air conditions in spite of which it developed the outward signs of rickets. These signs became progressive although it was given adequate vitamin and mineral supplements. During the winter of 1957–58 it became very sick but improved during the summer. It relapsed, however, during the autumn of 1958 and died suddenly.

EXAMINATION POST-MORTEM

Subcutaneous tissues and Peritoneum. The subcutaneous tissues and peritoneum were a lemon yellow colour and the animal was severely jaundiced. There was no doubt that death was due to jaundice.

Liver. The liver had the orange tint of a jaundiced liver. It was peppered throughout with white miliary nodules of small, but irregular, size. These appeared to be tuberculous but acid-fast organisms were not found in smears in spite of concentration methods.

Kidneys. The kidneys were very congested and had not the pale greasy look of feline kidneys. Nothing definite could be seen macroscopically although the appearances were of an acute glomerulo-nephritis.

Endocrines. The left adrenal gland showed white nodules as in the liver ; the right adrenal was normal. Both thyroids appeared a little large, otherwise normal. The parathyroids were not located.

HISTOLOGICAL FINDINGS

Liver. The liver showed a marked degree of cirrhosis, the fibrous trabeculae being thickened and increased in amount around the lobules. The architecture of the lobules was largely lost and the portal structures in particular difficult

to trace. The parenchymatous cords of hepatic cells were distorted and the sinusoids sinuous, widened and congested. Kupffer cells were very numerous and phagocytosis active ; indeed, phagocytic cells were very numerous throughout the organ. In the parenchymatous areas there were numerous very small tubercules consisting chiefly of round cells with a fibrous stroma. There were a number of giant cells associated with the tubercles. Ziehl-Neelsen stained sections showed acid-fast bacilli to be very scanty and many of them phagocytosed.

Kidney. There was a hyaline necrosis affecting all parts of the kidneys which involved virtual total destruction of the tubular epithelium and the glomeruli. The interstitial tissue was unaffected and appeared to have proliferated. The collecting ducts, also, were unimpaired. Ziehl-Neelsen stained sections of the kidney showed that there were scanty acid-fast bacilli present, more or less uniformly distributed through the section. There were no organised tubercles as such.

THE CONDITION OF THE SKELETON

The animal was affected with clinical rickets and the long bones were markedly bowed and fractured easily *post-mortem*. There was also a distinct ricketty ' rosary ', that is swelling at the junction of the ribs and the costal cartilages. The bones showed the typical osteoporosis associated with 'renal rickets ' together with the hyperplasia of osteoid tissue associated with the ' rubber bones ' condition.

BACTERIOLOGICAL STUDIES

In spite of the typical appearances of tuberculosis, acid-fast organisms were not readily found in tissue smears even after concentration by digesting the tissue in antiformin and centrifugation. As has been seen, a few acid-fast were demonstrated both in liver and kidneys in sections stained by Ziehl-Neelsen.

Cultures from the liver produced a dysgonic type of growth on media which did not contain glycerine. This would appear to establish the organism as having been of bovine type.

DISCUSSION

This case is of exceptional interest for a number of reasons. Osteodystrophic disease in lions has been known in most zoos for many years. Fiennes & Jones (1960, in press) have studied and reported on this condition and established that the disease is osteodystrophia fibrosa due to a low calcium/phosphorous balance in the diet. When the case in the puma was recognized as a supposed rickets syndrome, it was also supposed to be of dietary origin and every effort was made to correct this by provision of adequate vitamins and by giving sufficient calcium to correct any imbalance.

These efforts, as has been seen, were of no avail, and the disease progressed with an intermission during the summer until the death of the animal occurred during its second winter when only ten months old.

It is now established that the disease was osteodystrophia fibrosa cystica (' renal rickets '), which arose as a result of disease of the kidneys. The disease of the kidneys was a tubular nephritis due to diffuse tuberculous infection with organisms of bovine type.

' Renal rickets ' is a known disease in man and in some domestic animals, particularly the dog. More trouble is, however, experienced with this disease in certain groups of captive wild animals than in man and domestic animals. In particular, it is especially common in New World monkeys such as marmosets, capuchins and woolly monkeys, and in insectivores such as hedgehogs. In these species, the nature and cause of the nephritis is largely unknown and this adds to the interest of finding a case due to a known and ascertainable cause.

SUMMARY

1. A case of bovine tuberculosis is described in a ten month old captive puma which was born at Whipsnade Zoo.

2. The organs affected were the liver, kidneys, and left adrenal gland.

3. The disease was associated with severe symptoms of rickets which are supposed to have been secondary to tuberculosis of the kidneys. It was thus a case of osteodystrophia fibrosa of renal origin.

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THE NESTING SUCCESS OF THE HERON *ARDEA CINEREA* IN RELATION TO THE AVAILABILITY OF FOOD

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(With 3 figures in the text)

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INTRODUCTION AND METHODS

The heron *Ardea cinerea* is the only common member of the Ardeidae breeding in Britain. Many other species of Ardeidae occur further south ; most are predators of small vertebrates, especially fish, and large invertebrates ; they are thus especially numerous in wet tropical regions.

In Britain, herons breed in more or less well-defined colonies, but single nests are quite common, especially in Scotland and Wales. The size and distribution of these colonies depends to a large extent on the topography of the area ; more herons breed in low-lying river valleys and fens than in hilly country (Nicholson, 1929 ; Burton, 1954 ; Garden, 1958). Such a distribution seems correlated with the feeding grounds, fish being more abundant in lowland waters than in rivers and streams in hilly country. Herons feed along the edges of streams, rivers and pools, and also by the sea, and depend almost exclusively on food obtained in or near shallow waters where they can wade and probe.

In 1952, a study of the food of nestling herons was started at a heronry at Wytham, Berkshire, and in 1953 this work was extended to Buscot, Berkshire, about 20 miles west of Wytham, and to High Halstow, Kent, near the Thames

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estuary. An analysis of the food of nestling herons at each of these colonies for the years 1952–54 has already been published (Owen, 1955), and for completeness some of the data are summarised here. Subsequent to 1954, fewer food samples were collected and more attention was devoted to factors causing nestling mortality and to the behaviour of adult herons in the breeding season. This paper relates nesting success to the availability of food, and is based on data collected at Wytham in 1952–57, at Buscot in 1953–57 and at High Halstow in 1953–56. The number of nesting pairs at each of these three colonies in the years of study varied from 14–24 at Wytham, 30–40 at Buscot, and 87–129 at High Halstow. All the nests were 10–20 metres up in broad-leafed or coniferous trees, and thus the collection of data relating to egg-laying, clutch-size, hatching and fledging of the young, nestling weights and samples of food, involved extensive climbing. For this reason it was not possible to visit every nest in the heronries, and attention was concentrated particularly on those nests in the more accessible trees.

At Wytham the herons breed in a wood overlooking the rivers Thames and Windrush, which are bordered by water meadows intersected by numerous streams. Here they feed in slow-moving water, and some feed in flooded gravel pits which have been stocked with fish by anglers. Nine miles from Wytham, at Nuneham Courtenay, there is another heronry of about twenty nests, and it is possible that birds from this colony share some of their feeding grounds with the birds from Wytham. At Buscot the herons nest mainly on an island in a lake. The country around Buscot resembles that around Wytham, but the rivers and streams are smaller and flow faster. Most of the herons feed along the banks of the Thames and its tributaries. The heronry at High Halstow is situated in an oak wood on the edge of extensive drained marshes bordering the Thames estuary. Almost all the herons feed in the ditches which separate the reclaimed pastures, but a few feed on the salt marshes and on the tidal flats, and others feed at flooded clay and gravel pits.

Recoveries of herons ringed as nestlings at Wytham, Buscot and High Halstow showed that for the first three months after leaving the nest they moved away in all directions, but later recoveries suggested a southwesterly movement in autumn. Apart from three recoveries in France, none has been found outside Britain. These results are in agreement with the analysis of the recoveries of herons ringed in Europe (Rydzewski, 1956). In 1954–56 coloured celluloid rings were fixed to the legs of nestlings so that individual birds might be followed in the field. In 1958, a bird colour-ringed as a nestling at Wytham in 1956 was found breeding at North Aston, Oxfordshire, 13 miles north. Apart from this, there was no positive evidence as to where young herons eventually settled to breed.

FOOD OF NESTLINGS

Like many other fish-eating birds, herons readily regurgitate food when alarmed, and this was used as a method of obtaining food samples. In 1953–54 samples were collected about every two days at Wytham, once a week at Buscot and once a fortnight at High Halstow, but in later years samples were

collected less frequently. After examination the food was returned to the nest and there it was eaten again by the nestlings. Few samples were collected from nestlings younger than ten days old.

As the size of prey brought to the nestling herons varied considerably some allowance was made for this by dividing the prey into two categories :—

Large prey. This includes all eels *Anguilla anguilla* more than 15 cm. long, all other fish more than 10 cm. long, and all mammals and birds. Within this category there is some variation in size, but in general the different animals in the samples may be compared directly.

Small prey. This includes all fish smaller than the above, and all Amphibia, insects and Crustacea. Most of the insects were considerably smaller than even the smallest fish, but comparatively few were taken.

A complete list of all the food items found in the samples collected from nestling herons at Wytham, Buscot and High Halstow in 1952–57, and also details of a few other samples collected from other heronries in the upper Thames valley, is given in Appendix 1. (English names of fish, mammal and bird prey are also given). These figures are summarised as percentages in Tables 1 and 2 from which it is clear that there are differences in the proportions of the main kinds of food brought to nestlings at the three heronries. For a more detailed account of the food samples collected in 1952–54 see Owen (1955).

TABLE 1

Large prey in the food samples from nestling herons.

	Percentage occurrence		
	Wytham	Buscot	High Halstow
Cyprinidae and Percidae	88	64	22
Salmo trutta	1	19	—
Anguilla anguilla	5	6	65
Other fish	1	1	3
Mammals and birds	5	10	10
TOTAL ITEMS	992	228	231

TABLE 2

Small prey in the food samples from nestling herons.

	Percentage occurrence		
	Wytham	Buscot	High Halstow
Cyprinidae and Cobitidae	32	59	1
Gasterosteus aculeatus and *Pygosteus pungitius*	51	35	45
Other fish	2	2	3
Palaemonetes varians	—	—	47
Other Crustacea and Insecta	15	3	4
Others	—	1	—
TOTAL ITEMS	564	470	2251

Wytham

Fish of the familes Cyprinidae and Percidae comprised 88 per cent of the total large prey, and of these the river fish *Rutilus rutilus*, *Alburnus alburnus*, *Gobio gobio* and *Perca fluviatilis* were most frequent. Other Cyprinidae and *Acerina cernua* were occasionally taken. *Anguilla anguilla* was the only other fish frequently brought to the nestlings, and comprised 5 per cent of the total large prey. A few *Esox lucius* were taken, but only two *Salmo trutta*, both in 1953, and both at the same nest. *Arvicola amphibius* was the only common mammal and there were no birds. Of the small prey, as shown in Table 2, the fish *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Phoxinus phoxinus* were most frequent, very few immature fish of the larger species were found. Most of the insects were adult Odonata, especially *Agrion splendens*, and the larvae of aquatic Coleoptera.

Buscot

Compared with Wytham, many more *Salmo trutta* were taken (19 per cent of the large prey), and fewer Cyprinidae and Percidae (64 per cent). These differences may be related to the greater availability of *Salmo trutta* and the smaller numbers of Cyprinidae and Percidae in the rather faster flowing waters around Buscot. As at Wytham, *Rutilus rutilus* was the species most frequently taken, and there were also some *Gobio gobio* and *Perca fluviatilis*. *Alburnus alburnus*, numerous at Wytham, was not taken at Buscot. *Anguilla anguilla* was taken fairly frequently, and mammals, especially *Arvicola amphibius* were more common than at Wytham. Of the samples collected at Buscot many more than at Wytham contained small prey, but, as at Wytham, *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Phoxinus phoxinus* were the most frequent species. In addition, though only in 1954, *Nemacheilus barbatula* (Cobitidae) was common. These latter fish are rather larger than the average small prey and therefore only just come into this category. Other small prey comprised a few Odonata and aquatic Coleoptera, and six newts *Triturus* sp.

High Halstow

As would be expected from its position near the Thames estuary, the food brought to nestling herons at High Halstow differed markedly from the other two heronries. Table 1 shows that Cyprinidae and Percidae comprised 22 per cent of the total large prey, but only one species, *Scardinius erythrophthalmus*, was common ; apart from this there were only three *Gobio gobio* and one *Perca fluviatilis*. The important fish at High Halstow was *Anguilla anguilla* (65 per cent of large prey), which was caught by the adult herons in the numerous ditches draining the pasture lands near the heronry. The only large marine fish taken were five *Syngnathus acus* and one *Pleuronectes flesus*, both of which occur on tidal mud-flats in the estuary where adult Herons were occasionally seen feeding. *Arvicola amphibius* was again the commonest species of mammal taken. Table 2 shows the small prey ; *Gasterosteus aculeatus* and *Pygosteus pungitius* (in ratio 2 : 1) were numerous, but apart from a few immature *Scardinius erythrophthalmus* and *Anguilla anguilla* other species of

small fish were scarce in the samples. Crustacea, however, were common, especially the brackish and marine shrimp *Palaemonetes varians*, which comprised 47 per cent of the small prey taken. This shrimp occurs in ditches with water of low salinity as well as in the salt-marsh pools and estuary, and is exceptionally common at High Halstow. An estuarine shrimp, *Crangon vulgaris*, was much less frequently taken, and the crab, *Carcinus maenas*, although common in the area, was rarely eaten by the herons. Insects again comprised mainly Odonata and aquatic Coleoptera.

Thus, the difference in the proportion of the main species of prey brought to the nestling herons at each of the three heronries can largely be correlated with the position of the heronry in relation to the feeding grounds of the adult birds. Particularly striking is the importance of *Anguilla anguilla* and *Palaemonetes varians* at High Halstow, and the differences in the numbers of several species of Cyprinidae, *Salmo trutta* and small fish at Buscot and Wytham, despite the short distance of only 20 miles between these two heronries.

SELECTION OF FOOD BY HERONS

The food brought to nestling herons varied greatly in size, from small insects the size of *Notonecta* to fish 25 cm. long and mammals the size of *Mustela erminea* but most of the prey were well within these limits. Many of the whole fish

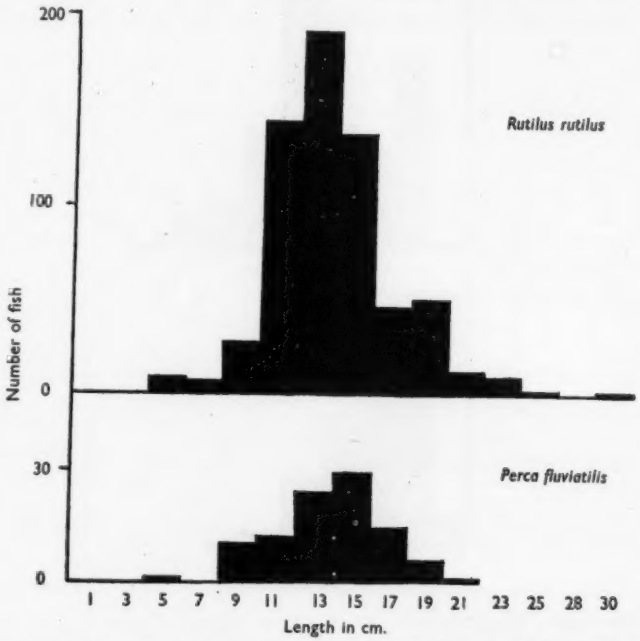

Fig. 1.—The length frequency-distribution of *Rutilus rutilus* and *Perca fluviatilis* brought to nestling herons at Wytham and Buscot.

found in the food samples were measured, and it was found that the adult herons took food selectively. Fig. 1 shows the length frequency-distributions of 642 *Rutilus rutilus* and 97 *Perca fluviatilis* brought to nestling herons at Buscot and Wytham. Fish of 10–16 cm. long were most frequently taken, smaller fish rarely, though these latter must have been more numerous on the feeding grounds than the larger individuals. Fish more than 20 cm. long were also not often taken, partly because they would be less common on the feeding grounds and partly because they would be too large to swallow comfortably. Length frequency-distributions of *Alburnus alburnus* and *Gobio gobio* brought to nestlings at Buscot and Wytham have been given elsewhere (Owen, 1955). Both these species do not often reach a greater length than 15 cm., and as most of those taken by herons were 10–13 cm. long, they were feeding on some of the largest fish available. Fig. 2 shows the length frequency-distribution of 172 *Anguilla anguilla* taken by herons at High Halstow, and also the lengths of 238 fish poisoned in a pool near High Halstow in August 1953. Assuming that these poisoned fish are a random sample of the sizes of fish available to the herons in this area, it is clear that fish 40–50 cm. long,

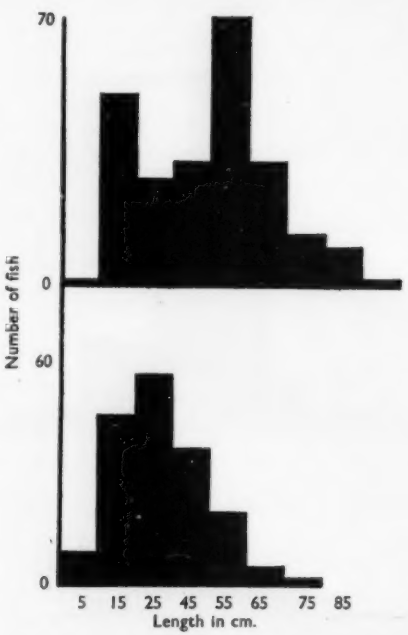

Fig. 2.—Upper figure : Length frequency-distribution of *Anguilla anguilla* poisoned in a pool near High Halstow, August 1953.
Lower figure : Length frequency-distribution of *Anguilla anguilla* brought to nestling herons at High Halstow.

although common, were not taken by the herons to any great extent, presumably because they are too large. Fish smaller than 10 cm. are away at sea and would therefore not be available to herons. It must be mentioned that the length frequency-distribution of *Anguilla anguilla* obtained from the pool near High Halstow does not agree with that given by Frost (1945).

Although, as shown, herons take the larger species of fish selectively by size, they also catch many fish belonging to small species (Table 2). Often food samples contained one or two large fish and many small fish, suggesting that the herons collected the small fish while waiting for larger prey.

Size of prey might also affect numbers taken. For instance at High Halstow in 1953 it was found that there was a sudden increase in the percentage of *Gasterosteus aculeatus* and *Pygosteus pungitius* taken at the end of June. This was presumably because fish born in that year had by then grown large enough for the heron to catch, whereas earlier they were too small. Previous to the last week of June the fish in the samples were all adults, but during that week the majority were young of the year (Owen, 1955).

The food samples collected indicate that adult herons do not bring smaller prey for newly-hatched young. Instead the food for such young was partially digested and then fed in small quantities.

The fact that herons are unable to catch the smallest and the largest fish in an area means that besides being restricted to shallow water for feeding, they are also restricted to catching certain classes of the available fish.

BREEDING SEASON

Table 3 shows the number of clutches started in 10-day periods commencing 1st March. All repeat clutches after the loss of the first clutch (which are normal until mid-May and occasional later) have been omitted. Table 3 shows that laying normally commenced in early March and that most clutches were started between 11th March and 9th April. The timing of the breeding season is comparable with that of the Rook *Corvus frugilegus* (Lockie, 1955), but the laying of the eggs is spread over a longer period. In 1955, breeding was 10 days later than in 1954, and in 1957 it commenced exceptionally early. These differences can be correlated with the mean air-temperatures just prior to egg-laying, 1954 being warmer than 1955, and 1957 being an exceptionally mild early spring, causing many birds in southern England to breed earlier than usual.

TABLE 3

Egg-laying dates of the heron.

Dates	Buscot					Wytham				High Halstow		Total
	1953	1954	1955	1956	1957	1953	1954	1955	1956	1954	1955	
1–10 March		1			6					2		9
11–20 March	2	6		1	2	2	2	4		15		34
21–30 March	8	10	3	9		6	5	3	2	8	15	69
31 March–9 April	7	3	13	3		3		3		1	17	50
10–19 April			5	2		2			3		7	19
20–29 April	1			1								2

Each year, at Buscot, Wytham and High Halstow, some birds commenced breeding in high inaccessible trees earlier than the dates given in Table 3, and if it had been possible to examine nests in these trees there would have been more records of early clutches. It is not known why breeding should be earlier in these high trees.

It is now generally agreed that, in temperate regions, many species of birds lay their eggs at such a time that the young are in the nest when food is most available. Broods of young herons hatch about thirty days after the laying of the first egg and are therefore in the nest from the end of April until the middle of June. Later broods of young are due to repeat clutches after the first has been destroyed. As will be shown later, many young herons died of starvation in the nest, and this alone suggests that food is likely to be an important ultimate factor controlling the timing of the breeding season. The availability of food could well account for the early nesting in the heron, for, as is well known, there is in May a movement of many species of fish, especially Cyprinidae, into shallow water for spawning. Here they would be more available to feeding herons than in the deeper water. Table 4 shows

TABLE 4

Seasonal variation in the proportion of large prey brought to nestling herons at High Halstow, 1953–56.

	Percentage occurrence		
Dates	*Anguilla anguilla*	*Scardinius erythrophthalmus*	Others
15–30 April	93	7	—
1–15 May	81	16	3
16–31 May	44	42	14
1–15 June	78	11	11
16–30 June	66	7	27

Note : ' Others ' were chiefly *Arvicola amphibius*.

TABLE 5

Seasonal variation in the proportion of some large prey brought to nestling herons at Buscot, 1953–57.

	Percentage occurrence			
Dates	*Salmo trutta*	*Rutilus rutilus*	Other fish	Mammals
15–30 April	38	31	8	23
1–15 May	36	47	18	—
16–31 May	7	63	21	9
1–15 June	16	42	21	21
16–30 June	17	40	26	17
1–15 July	19	43	29	9

the seasonal changes in the proportion of some kinds of large prey brought to nestlings at High Halstow. The cyprinid, *Scardinius erythrophthalmus* was most numerous in the period 16–31 May and many of those caught by the herons were spawning females. Both earlier and later than this *Anguilla anguilla* was the most common prey, and the increase in other prey, chiefly *Arvicola amphibius*, later in the season might have been due to a decrease in the availability of fish.

Similarly, at Buscot, there were seasonal changes in the food, as shown in Table 5. *Salmo trutta* comprised 38 per cent and 36 per cent of the total large prey brought to the nestlings in the first two periods, and the fall to 7 per cent in the next period coincides with the greater availability of the Cyprinidae, especially *Rutilus rutilus*. Thereafter the proportion of *Rutilus rutilus* decreased, though other Cyprinidae were still important, and there was a tendency for *Salmo trutta* to return later in the season. Mammals were more often taken earlier and later in the season than at any other time. At Wytham, where the feeding grounds are richer, there was little seasonal change in food, as shown in Table 6. Here, apart from a drop to 73 per cent in early July, the proportion of Cyprinidae and Percidae remained at 85–91 per cent throughout the season when the herons were in the nest. There was the usual tendency for mammals to become more numerous late in the season, and there is a sharp, but unexplained, increase in the proportion of *Anguilla anguilla* in early May.

TABLE 6

Seasonal variation in the proportion of some large prey brought to nestling herons at Wytham, 1952–57.

	Percentage occurrence			
Dates	Percidae and Cyprinidae	*Anguilla anguilla*	Other fish	Mammals
15–30 April	91	—	—	9
1–15 May	85	13	1	1
16–31 May	90	5	3	2
1–15 June	85	6	1	8
16–30 June	87	1	2	10
1–15 July	73	7	—	20

Note : ' Other fish ' includes 14 *Esox lucius*, nine of which were taken in the period 16–31 May.

These changes in the proportion of some species of prey reflect changes in their availability in or near shallow water where the adult herons feed. It is, of course, only possible to demonstrate seasonal changes in availability of food when one prey species is replaced by another, and frequently there must also be a decrease in the availability of one species which is not balanced by the increase in another. Thus, a species of fish might be more easily caught at one time of the year than at another ; we now need to know exactly how easy it is for a heron to catch a fish at a given time.

A factor which would presumably influence the numbers of fish taken is the seasonal growth of aquatic vegetation in late spring and early summer. This would make feeding in shallow water more difficult later in the season than earlier. The ditches around High Halstow were by late June almost completely choked with vegetation and there can be little doubt that early nesting is advantageous if the young are in the nest before this seasonal growth occurs.

Possibly there are also other factors occurring annually which affect the availability of food to the heron.

CLUTCH-SIZE

The clutch-size of the heron was determined by repeated visits to a nest during and just after the laying of the clutch, care being taken to exclude all partially destroyed clutches, such as those that had been attacked by predators. Table 7 shows the distribution of clutch-sizes. Clutches of three to five were most frequent, clutches of two were rare, and clutches of six were not recorded, though there are records in the literature. No annual differences in clutch-size were found, and the differences between the averages for each heronry shown in Table 7 are slight and not statistically significant.

TABLE 7

Clutch-size of the heron.

	Number of clutches		
Clutch-size	Wytham	Buscot	High Halstow
2	3	1	—
3	8	16	17
4	30	40	66
5	9	7	23
Average	3·9	3·8	4·1

Notes : (i) Figures are for all years except Buscot 1953, which has been omitted because of partial predation of some clutches.

(ii) The differences between the averages are not statistically significant.

Repeat clutches, after the destruction of first attempts, almost always occurred until about mid-May and occasionally later ; often a bird would lay three or four clutches in one season which would be successively destroyed by crows (*Corvus corone* and *C. monedula*). The size of repeat clutches was not on the average different from that of first attempts, but some repeats by an individual female were higher and some lower than the first attempt. The only certain second brood, after the first brood had been successfully raised, was at Buscot in 1954. This was a clutch of four, the first clutch having been three.

It was not possible to say for certain whether female herons tended to lay the same clutch-size in different years, as the adult birds were not marked individually, but the fact that a female might vary its clutch-size within one year shows that it is not genetically fixed. In one instance, at Wytham, a female which produced exceptionally long eggs laid a clutch of four in 1955 and five in 1956 ; in 1957, another female, but not necessarily another male, occupied the same nest.

Herons normally first breed when two years old, but one-year old birds, recognised by their grey appearance and short crests, frequently visited the heronries and showed reproductive behaviour. They even built small nests, and in 1954, at Buscot, a first year bird, by its behaviour a female, mated with an adult whose mate had disappeared and whose first clutch had been destroyed. Two eggs were laid by this female, but although the young hatched they did not survive. In 1957, at Wytham, a first year bird, of unknown sex, mated with an adult bird and five eggs were laid from which two young were sucessfully raised.

Thus, judging on the records given here, the clutch-size of the heron, unlike that of many small birds, is stable, and does not vary adaptively with season and locality. Assuming clutch-size to be inherited, one would expect clutches of five to predominate over those of four as they would produce more young. The fact that they do not become more common suggests that they are at a selective disadvantage.

WEIGHTS OF NESTLINGS

Like many other large birds, such as hawks and owls, the heron starts incubating its eggs before the clutch is complete. Incubation starts gradually, and normally commences on the second or third, occasionally the first, egg of the clutch. At Wytham and Buscot there was a tendency for incubation to start on the first egg, in clutches of three, on the second in clutches of four and on the second or third egg in clutches of five, but the figures obtained are not significant, partly because of the gradual start of incubation. No attempt was made to determine the start of incubation in clutches at High Halstow. Eggs are laid at an average interval of two days and the young herons hatch at intervals of approximately two days.

Nestling herons were periodically weighed and by choosing different brood sizes and different years, variations in the growth rate were detected. Young herons weigh about 45 grams on hatching, they grow rapidly, so that in a brood of five, the first nestling to hatch may weigh 400 grams by the time the last egg has hatched. In unfavourable years for food such differences in weight between the members of a brood were maintained, but in good years they were less apparent after a short period in the nest. Thus, in unfavourable years, the last hatched young were at a disadvantage so far as receiving food was concerned, and, as will be shown later, this frequently led to death from starvation. At the age of three and a half weeks, in an average year, the young herons have normally reached their peak weight, being as heavy or rather heavier than adults (1100–1300 grams) ; only exceptionally did birds die in the nest after reaching 1000 grams.

Appendix 2 shows a selected series of weights of birds from different brood sizes and in different years. The fate of each young heron in a brood can be followed by watching its growth rate, as shown by the weights. In the three broods weighed at Wytham in 1953 the last hatched young was at first at a disadvantage compared with the first hatched, but eventually it caught up in weight and survived. But in broods in which mortality occurred, a brood of five and a brood of four at High Halstow in 1955 and a brood of five at Wytham in 1955, the smaller nestlings gained weight more slowly and eventually died. The weights of the brood of five at Wytham are plotted in Fig. 3. Two nestlings hatched on 2nd May, a third on 3rd May, a fourth on 5th May and the last on 8th May. The first two grew normally, as did the third until 12th May, when its growth rate fell off. The fourth bird grew more slowly and died of starvation about 20th May. Almost immediately the third nestling put on weight and soon caught up with the first two, indicating that the presence of the fourth nestling restricted the growth of the third bird. As shown in Fig. 3, the last hatched nestling lived only a week.

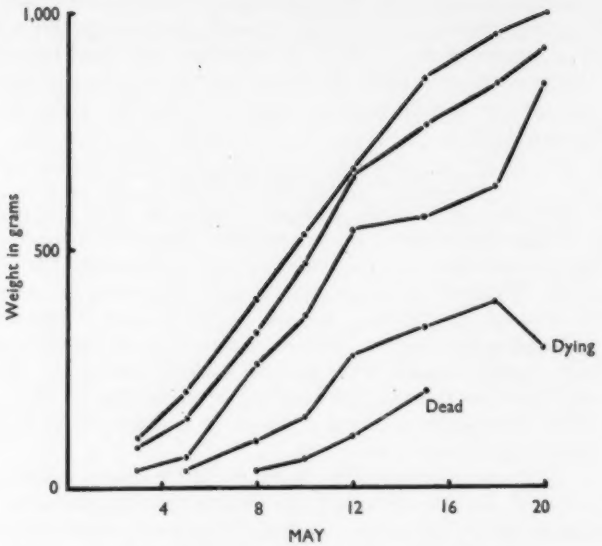

Fig. 3.—Weights of a brood of nestling herons at Wytham, 1955.

Figures given in Appendix 2 show the growth of five broods of herons of brood sizes one to five respectively, all weighed on the same dates at High Halstow. The broods of one to three grew normally, but in the brood of four the third and fourth birds did not grow as rapidly as the birds in the brood of three, and the fourth bird eventually died. In the brood of five, the third, fourth and fifth birds grew very slowly and all three eventually died, the smallest first. Thus, in this instance when five broods were followed simultaneously through the critical growing period, the broods of one to three were found to be completely successful, the brood of four lost one young, and the brood of five lost three young. Feeding conditions through the period must have been similar for each pair of adult herons and some food samples confirmed this, and the mortality in the larger broods was evidently due to food shortage caused by the greater number of young in the nest.

The adaptive value of asynchronous hatching is that when food is scarce, the smallest young in the nest die of starvation, but when food is more plentiful all the young are raised. If all the young were hatched at the same time they would all be of the same size in the nest and each would run an equal risk of occasional deprivation, so that all might be so weakened as to die.

MORTALITY OF NESTLINGS

Table 8 shows the mortality of nestling herons from the time of hatching until leaving the nest. The brood-size was not always the same as the clutch-size as there were often some eggs that failed to hatch and some that were lost to predators and unknown causes. A few young also died during hatching,

and a few broods of nestlings were completely destroyed by predators, chiefly carrion crows *Corvus corone* and jackdaws *C. monedula*. These have all been excluded from Table 8. The nestling losses considered here are thus partial losses of a brood occurring after the first, and usually before the fourth week, after hatching. As already shown, young herons hatch asynchronously and in every case where nestlings died in a brood they were the smallest.

TABLE 8

Percentage mortality of broods of herons that started as three, four or five young.

	Number of broods	Young hatched	Young raised	Percentage dying	Number of broods losing two or more young
Buscot					
1953	9	31	27	13	—
1954	9	34	23	32	3
1955	14	54	29	46	4
1956	12	44	43	2	—
1957	6	21	15	29	2
Wytham					
1952	3	10	9	10	—
1953	8	32	31	3	—
1954	3	12	10	17	—
1955	6	23	19	17	1
1956	4	16	15	6	—
High Halstow					
1953	14	52	36	31	4
1954	13	50	32	36	4
1955	24	93	78	16	2

Notes : (i) Broods of two were completely successful in all years and at all heronries.

(ii) Only two broods were examined at Wytham in 1957, and these, both of three young, were completely successful.

(iii) Broods of 3, 4 and 5 were similarly distributed in each year and at each heronry (see Table 7 for distribution of clutch-sizes).

As shown in Table 8, the number of young dying at Buscot in each of the years 1953–57 varied from 46 per cent in 1955 to 2 per cent in 1956. The differences in mortality between 1955 and 1956, 1955 and 1953, and 1954 and 1956 are significant at the 5 per cent level, while the difference between 1956 and 1957 is almost so.

The mortality of nestlings at Wytham in the years 1952–56 (Table 8) shows a similar trend to that at Buscot, but with a variation of only 3 to 17 per cent. As fewer nests were available at Wytham than at Buscot, and the annual variation in mortality not as marked, there are no significant differences between any of the years. At High Halstow, with an annual variation in mortality of 16 to 30 per cent, as shown in Table 8 the differences are again not significant, but the difference between 1954 and 1955 is nearly so. Comparing the same years in each of the three heronries, there is no significant difference

between Wytham and Buscot, but adding all the years together, 26 per cent of the young hatched at Buscot died, whereas at Wytham only 10 per cent died. As can be seen in Table 8, the nestling mortality at Wytham in each year followed the same trend as at Buscot. In 1955, significantly more young died at Buscot than at High Halstow.

Whenever dead nestlings were examined they showed signs of having died of starvation. First, it was always the smallest young of a brood that died, which would be expected if there was a shortage of food. Secondly, the stomachs of the dead nestlings were always empty. Thirdly, dead nestlings were thin and the pectoralis major muscles were poorly developed. Fourthly, as shown below, from observations made at feeding times it was clear that the larger young received more food than the smaller, and often there was a severe struggle when an adult bird arrived back at the nest with food.

For instance, on 8th June 1953, at Wytham, three food samples were collected successively from a brood of four immediately after they were fed by the adult herons. The first meal was taken almost entirely by the largest nestling, the second meal was shared among the three largest, the largest receiving the most, and the third meal was again shared among the three largest, but this time the third bird received the most. During this period (three-and-a-half hours) the smallest bird did not receive any food and was three times pushed out onto some branches by the other members of the brood. Similar observations were made on other broods of herons. Comparable results were obtained by Lockie (1955) with a brood of jackdaws *Corvus monedula*, another bird that has young of different sizes in the nest.

It therefore seems certain that starvation was the cause of mortality among these broods of herons at Wytham, Buscot and High Halstow. There was no evidence of disease, harmful endoparasites were not common, and apart from a few *Carnus hemapterus* (Diptera), blood-sucking ectoparasites were absent ; *Lynchia ardeae*, the common dipterous parasite of herons and similar birds, is apparently absent from herons breeding in Britain (Owen, 1957). Predation affected only eggs and very small young, and whenever small young were killed by a predator, the whole brood was destroyed. Such losses were infrequent and are not included in Table 8 which gives only partial losses from a brood.

On the feeding grounds of the adult herons near Wytham and Buscot an important factor affecting the availability of food seems to have been the amount of rain in May. This is the time of year when most young herons are growing rapidly and therefore likely to be in greatest need of food. Table 9 shows the rainfall at Oxford and the percentage mortality of nestlings at Buscot for the years 1953–57. In 1955, the correlation of 46 per cent nestling mortality with 114 mm. of rain in May (21 wet days) is striking when compared with the 2 per cent mortality in 1956 with only 8 mm. of rain (8 wet days). As shown in Table 9 higher mortality of nestlings in the other years was also associated with more rain.

Rain falling causes mud and earth to be carried into rivers and streams and results in muddy water, increases the volume and rate of flow of the water, and when actually falling causes a surface ripple. These factors contribute

TABLE 9

Mortality of nestling herons at Buscot, 1953–57, and rainfall in May.

	Rainfall in May at Oxford (20 miles E. of Buscot) (in mm.)	Percentage young dying
1953	41	13
1954	54	32
1955	114	46
1956	8	2
1957	40	29

toward making fishing by sight difficult, and there seems little doubt that this accounts for the great difference in nestling mortality between 1955 and 1956. Further, the heavy rain in 1956 was also partly associated with the low mean temperatures, and this may have lowered the resistance of the nestling herons. No correlation between the amount of rain and nestling mortality could be found for High Halstow, but the annual differences in rainfall and mortality were not as great as they were at Buscot in 1955 and 1956. Moreover, the feeding places at High Halstow are largely small ditches where the water level does not rise and fall so much as in the rivers.

The higher average mortality at Buscot (26 per cent) compared with Wytham (10 per cent) seems correlated with poorer feeding areas. Small fish, *Salmo trutta*, and mammals were more frequent in the samples from Buscot, and Cyprinidae, which are evidently more readily caught, scarcer. In addition, the Wytham heronry is situated within easy reach of a complex river system and there are thus more possible feeding places than at Buscot. The herons at High Halstow depend largely on *Anguilla anguilla* and any changes in its availability might affect nestling mortality, but unfortunately nothing is known of factors affecting the availability of this fish to the heron. Not enough food samples were collected at High Halstow in 1955 to say whether the food differed from that in 1954 ; these were the two years of greatest difference in nestling mortality.

Table 10 shows the survival of nestlings in relation to brood size at the time of hatching. Broods hatching only two nestlings were completely successful at all three heronries, broods starting as three lost a few young in the bad years, but none in the good years, while broods starting as four lost more young, especially in the bad years. Not enough broods of five are available for analysis from Wytham and Buscot, but at High Halstow the overall success of broods of five was only just better than broods of four, and in 1955 it was slightly worse, eleven broods of four raising an average of 3·5 young each and five broods of five raising an average of 3·4 young. Hence, although there was a heavier mortality in the bad years among the higher broods the average number of young raised was higher than in the smaller broods, except in the broods of five at High Halstow in 1955. As mentioned already, there is evidence that less food was available at Buscot than at Wytham and the figures given in Table 10 support this, broods of four being more successful at Wytham than at Buscot.

TABLE 10

Survival of nestling herons in relation to brood size.

Brood size at time of hatching	Number of broods	Average number of young raised per brood
	Buscot, 1953–57	
2	14	2·0
3	17	2·7
4	32	3·0
	Wytham, 1952–57	
2	10	2·0
3	10	2·9
4	14	3·8
5	2	(3·5)
	High Halstow, 1953–55	
2	5	2·0
3	16	2·6
4	28	2·9
5	7	3·1

MORTALITY AFTER LEAVING THE NEST

Recoveries of herons ringed as nestlings showed no significant difference in survival after leaving the nest between Buscot, Wytham and High Halstow, but the survival rate after leaving the nest differed in the different brood sizes. In Table 11, recoveries after 1st September are expressed as a percentage

TABLE 11

Brood size and survival after leaving the nest in herons.

Brood size at time of leaving the nest	Number of nestlings ringed	Recovered after 1st September	Per cent recovered
1	38	7	18·4
2	110	27	24·5
3	195	28	14·4
4	108	14	12·9

Notes : (i) The differences between the number of recoveries from brood sites 2 and 4 and 2 and 3 are statistically significant, the 2×2 χ^2 values being 4·78 and 4·94, respectively.

(ii) This analysis does not take into account any effect due to mortality in the nestling stage, which, however, normally occurs before the fourth week of the eight week nestling period. If there were more figures available this table would be subdivided to show initial as well as final brood size.

of the total nestlings ringed in broods that raised 1 to 4 young. It is assumed that any ill-effects derived from being a member of a particular brood size have disappeared by 1st September, and thus the percentages of recoveries after this date really refer to the numbers of birds known to be alive. Table 11 shows that the percentage of birds recovered (i.e. known to be alive) after 1st September was higher in the smaller broods of one to two than in the larger

broods of three to four. This suggests that the small broods are at a selective advantage over the large broods in the period from leaving the nest until 1st September. The twelve recoveries from this period are insufficient for analysis, but four came from broods of one to two and eight from broods of three to four. A similar analysis, based on all recoveries of herons ringed in Britain gave inconclusive results (Lack, 1949), almost certainly because there was further nestling mortality after the birds had been ringed.

SUMMARY

1. The food of nestling herons *Ardea cinerea* was studied at three heronries in the Thames valley in the years 1952–57. At Buscot and Wytham, Berkshire, fish of the families Cyprinidae and Percidae formed the chief food, but at Buscot many *Salmo trutta* were also eaten. At High Halstow, Kent, in the Thames estuary, *Anguilla anguilla*, *Scardinius erythrophthalmus*, small fish of several species, and shrimps, formed the chief food of the nestlings. It was found that herons caught fish selectively, avoiding both small and large individuals.

2. At Buscot and at High Halstow, but not at Wytham, there were seasonal changes in the proportion of certain prey species which suggest that the heron lays its eggs at such a time that the young are in the nest at the period of maximum availability of food.

3. Young herons hatch asynchronously, and in years of mortality it was always the smallest last-hatched young that died. It is shown that the adaptive value of asynchronous hatching is that when food is short the smallest young in the nest die, but when food is more plentiful all the young are raised.

4. The average clutch-size of the heron did not vary significantly, but the survival of young after hatching differed markedly over the six years, and also in the different heronries. These differences were due to starvation, the availability of food to the adult herons being affected by the amount of rainfall and possibly other factors. The percentage of the young surviving was higher in the smaller broods, both in the nest and after fledging.

ACKNOWLEDGMENTS

I am grateful to D. F. Dorward, J. D. Lockie and G. C. Phillips for much help with the field work, and to Dr. D. Lack and G. C. Phillips for discussion and criticism of the results. Rainfall figures were kindly supplied by the Department of Geography, Oxford University.

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APPENDIX 1. THE FOOD OF NESTLING HERONS

LARGE PREY

	Wytham	Buscot	High Halstow
Number of food samples	313	131	160
FISH			
Salmo trutta (trout)	2	45	—
Esox lucius (pike)	14	3	—
Cyprinus carpio (carp)	2	5	—
Gobio gobio (gudgeon)	83	12	3
Tinca tinca (tench)	7	4	—
Rutilus rutilus (roach)	518	109	—
Scardinius erythrophthalmus (rudd)	—	—	46
Alburnus alburnus (bleak)	149	—	—
Anguilla anguilla (eel)	57	14	151
Perca fluviatilis (perch)	94	10	1
Acerina cernua (ruffe)	13	1	—
Syngnathus acus (great pipe fish)	—	—	5
Pleuronectes flesus (flounder)	—	—	1
Unidentified	—	—	1
MAMMALS			
Arvicola amphibius (water vole)	42	16	13
Microtus agrestis (field vole)	1	2	2
Talpa europaea (mole)	4	3	1
Neomys fodiens (water shrew)	1	2	2
Sorex araneus (common shrew)	5	—	—
Sorex minutus (pygmy shrew)	—	1	—
Mustela erminea (stoat)	—	—	1
BIRDS			
Fulica atra (coot)	—	1	—
Gallinula chloropus (moorhen)	—	—	3
Vanellus vanellus (lapwing)	—	—	1
Total large prey	992	228	231

Notes: (i) It is possible that a few *Scardinius erythrophthalmus* and *Leuciscus leuciscus* (dace) have been included under *Rutilus rutilus* in the figures for Buscot and Wytham. This is because of the difficulty in identifying these very similar species after partial digestion in the stomachs of the nestling herons.

(ii) Two of the *Gallinula chloropus* and the *Vanellus vanellus* were chicks.

(iii) A few food samples were collected from four other heronries in the upper Thames

valley, all within 30 miles of either Buscot or Wytham. The following species of large prey were identified : Fish : *Rutilus rutilus* (14), *Gobio gobio* (9), *Anguilla anguilla* (2), *Perca fluviatilis* (4) ; Mammals : *Arvicola amphibius* (2), *Talpa europaea* (1) ; Bird : *Anas platyrhynchos* (1 mallard duckling).

SMALL PREY

	Wytham	Buscot	High Halstow
FISH			
Phoxinus phoxinus (minnow)	158	195	—
Rutilus rutilus (roach)	21	13	—
Scardinius erythrophthalmus (rudd)	—	—	10
Gasterosteus aculeatus and *Pygosteus pungitius* (3-spined and 10-spined sticklebacks)	285	162	1031
Anguilla anguilla (eel)	—	—	52
Cottus gobio (bullhead)	13	11	—
Nemacheilus barbatula (stone loach)	—	68	—
Gobius minutus (goby)	—	—	11
CRUSTACEANS			
Palaemonetes varians	—	—	1059
Crangon vulgaris	—	—	38
INSECTS			
Dytiscus sp.	21	3	31
Agrion splendens	41	1	2
OTHERS			
Crustaceans, Insects, Amphibians	25	17	17
Total small prey	564	470	2251

Notes : (i) ' Others ' were mainly insects (see Owen, 1957, for list) ; there were also six newts *Triturus* sp. from Buscot, and a few Crustacea (*Gammarus* spp., *Carcinus maenas* and *Astacus fluviatilis*).

(ii) *Gasterosteus aculeatus* was about twice as common as *Pygosteus pungitius* at High Halstow, and predominated at Wytham and Buscot.

(iii) Thirty-nine *Dytiscus* sp. were larvae.

APPENDIX 2. SOME SELECTED WEIGHTS OF NESTLING HERONS

Nestlings were weighed in a cotton bag attached to a spring balance. The bag was weighed each day and the accuracy of the balance was checked periodically ; it was accurate to $\pm$ 5 grams. The amount of food in the stomachs fo the nestlings at the time of weighing caused some variation, but birds with completely full stomachs were not weighed.

1. Five broods of brood sizes 1–5, High Halstow, 1955.

		Weights (in grams)			
		8 May	15 May	22 May	28 May
Brood 1	1st nestling	325	775	1250	1510

APPENDIX 2. (continued)

		8 May	15 May	22 May	29 May
2	1st nestling	195	680	950	1430
	2nd „	120	550	850	1260
3	1st nestling	65	365	900	1360
	2nd „	45	245	750	1190
	3rd „	40	185	645	1150
4	1st nestling	370	765	1025	1330
	2nd „	305	670	825	1150
	3rd „	205	520	575	830
	4th „	90	370	450	460
5	1st nestling	395	645	1075	1590
	2nd „	335	605	900	1450
	3rd „	215	340	465 (dead)	
	4th „	140	295	420 (dead)	
	5th „	45	130	(missing-dead)	

2. Brood of five, Wytham, 1955.

	Weights (in grams)							
	3/5	5/5	8/5	10/5	12/5	15/5	18/5	20/5
1st nestling	108	205	400	535	670	860	950	995
2nd „	90	155	332	470	650	760	845	920
3rd „	42	65	265	360	545	570	635	845
4th „		40	100	155	280	340	395	295 (dying)
5th „			40	77	110	205 (dead)		

Note : The nestlings in this brood hatched on the following dates : 2 May (2), 3 May (1), 5 May (1) and 8 May (1).

3. Brood of four, Wytham, 1953.

	Weights (in grams)												
	22/4	24/4	26/4	1/5	4/5	6/5	8/5	10/5	12/5	15/5	17/5	19/5	21/5
1st nestling	45	85	125	410	645	805	875	980	1065	1230	1365	1450	1400
2nd „	45	80	120	400	605	778	785	960	1030	1205	1290	1300	1350
3rd „		70	100	320	570	715	765	955	1005	1155	1240	1250	1300
4th „			55	153	305	415	525	715	705	925	1040	1150	1100

Note : The nestlings in this brood hatched on the following dates :—22 April (2), 23 April (1) and 25 April (1).

4. Brood of four, Wytham, 1953.

	Weights (in grams)												
	5/5	7/5	9/5	11/5	13/5	15/5	17/5	19/5	21/5	23/5	25/5	27/5	29/5
1st nestling	41	85	140	235	335	493	585	710	935	1010	1120	1180	1230
2nd „	39	80	135	210	305	480	580	695	800	950	1020	1100	1230
3rd „		47	80	145	205	340	390	520	605	715	840	950	1005
4th „			45	80	120	215	280	305	425	655	740	880	930

Note : The nestlings in this brood hatched on the following dates : 5 May (2), 7 May (1) and 9 May (1).

5. Brood of three, Wytham, 1953.

	Weights (in grams)										
	3/5	5/5	7/5	9/5	11/5	13/5	15/5	17/5	19/5	21/5	23/5
1st nestling	55	135	250	365	520	625	805	970	970	1110	1160
2nd „	50	130	240	345	475	605	755	915	950	1000	1150
3rd „		67	130	220	355	485	655	805	900	975	1110

Note : The nestlings in this brood hatched on the following dates : 2 May (2) and 4 May (1).

OBSERVATIONS ON THE ORIENTATION AND FEEDING OF THE COPEPOD *SABELLIPHILUS ELONGATUS* M. SARS ON ITS FAN-WORM HOST

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(With 1 plate and 1 figure in the text)

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INTRODUCTION

The recent series of papers by Bocquet & Stock (1956 *et seq*) and by Gooding (1957) has added a number of new species to the already extensive list of copepods known to be associated more or less intimately with marine invertebrates. Increasing knowledge of host diversity has emphasized the remarkable versatility of copepods in the role of associative organisms, and indicated a rich field for more detailed investigation. Bocquet (1953) has, in fact, already touched upon the probable course of events leading to speciation in the annelidicolous genus which is the subject of this paper. Our present information, however, on the general biology of these crustaceans is so fragmentary that tentative conclusions only can be drawn. The observations recorded here are an attempt to fill in a few details regarding one such copepod—the cyclopoid *Sabelliphilus elongatus* M. Sars, which occurs on the branchial crown of the fan-worm *Sabella pavonina* Savigny.

The genus *Sabelliphilus* was erected in 1862, and is now known to include at least two species, *S. elongatus* and *S. sarsi*. The former lives on the branchial crowns only of *Sabella pavonina* and *Sabella spallanzanii* (Viviani) whilst mature females of the latter are restricted to the body region of *S. spallanzanii*, although copepodid stages can be found on the crown. Structurally, the two species differ only in very minor details. The genus was placed by G. O. Sars (1918) in the family Lichomolgidae although several features distinguish it from more typical members of that group, notably the narrow, elongate body and the specialized nature of the antennules and antennae. Ovigerous females of *S. elongatus* attain a length of about 1·75 mm. and bear egg-sacs

which are longer and more cylindrical than those usually carried by lichomolgids. The male, which is appreciably smaller than the female, has been described recently by Lang (1949). The host worm, *Sabella pavonina*, is found at low tide in several areas of Strangford Lough, Co. Down, and a fair proportion of those collected carry specimens of *S. elongatus* on the branchial filaments. Thus in October, 1958, twenty-three out of twenty-six worms were infected (88 per cent), the largest number of copepods occurring on a single host being eighteen. Both polychaet and crustacean thrive under laboratory conditions, the latter breeding readily and thus ensuring a steady supply of material.

Quite a number of the *Sabelliphilus* collected carry on the ventral surface what appear to be the phoretic cysts of an apostomatous ciliate. *Foettingeria actiniarum* Caullery & Mesnil was recorded from the Strangford region by Williams (1954) in *Actinia equina*, a primary host which is common in the area where the sabellids were collected. Copepods suspected of infection were fed to young translucent anemones, and in several cases small objects (young trophonts ?) were subsequently seen moving rapidly within the gastrovascular cavity and tentacles in the manner described by Chatton & Lwoff (1935). Time did not permit the obtaining of absolutely conclusive evidence (since the full growth of the trophont requires several weeks) that *Foettingeria* was, in fact, the ciliate involved, though this seems very probable. One would imagine that tomites encysting on *Sabelliphilus* would stand a negligible chance of completing their life cycle, since the niche occupied by this copepod would guarantee virtual immunity from predation by *Actinia*. However, Chatton & Lwoff have shown that encystment may take place on crustaceans even less likely as objects of actinian nutrition. It may be that the ciliary current produced by the fan-worm is partly responsible for bringing the minute tomites within, so to speak, striking distance of this somewhat improbable host.

ORIENTATION, ATTITUDE AND BEHAVIOUR

Recent work by Llewellyn (1956) on the gill-infesting trematodes of marine fish, and by Gotto (1957) on the ascidicolous copepod *Ascidicola rosea*, has emphasized the significance of what Llewellyn calls " an exacting topographical relationship between parasite and host ". A similarly precise relationship is strikingly illustrated by *S. elongatus* on *Sabella*.

Almost without exception, the adult copepods align themselves along the outer (abfrontal) sides of the branchial filaments with their heads pointing towards the mouth of the worm's tube (Pl. 1, fig. 1). This is clearly not a geotactic effect, since the widely radiating filaments of a sabellid fan may assume any position relative to the substrate. It is equally obvious that phototaxis cannot be invoked to explain this curiously constant orientation. The assumption might perhaps be made that it confers some advantage as regards feeding, but again, for reasons adduced below, this seems most unlikely. An explanation can, however, be found, when the copepod's method of attachment is considered in relation to the structure and movements of its host.

The exceptionally powerful antennae are the organs utilised to grasp the filaments. Only one filament is gripped at a time, and one copepod per

filament is the general rule, although quite often two, or, sometimes, three copepods may be found on a single filament. The fringing pinnules are grasped very occasionally by adults, but more frequently by the copepodid stages. The antennae, to quote Sars' description (*loc. cit.* p. 188) are " unusually strongly built, 4-articulate, the first two joints very massive and forming with each other a geniculate bend ; second joint exhibiting inside a longitudinal crest divided into five very strong teeth ; third joint armed at the end anteriorly with a strongly uncinate claw ; terminal joint with three similar claws accompanied by a number of curved setae ".

These appendages (Fig. 1 c), whilst thus conforming in general pattern to those of other lichomolgids, are highly specialised in their detailed structure for maintaining a firm hold on the crown of *Sabella*. The depth of each branchial filament, measured from the convex abfrontal surface to the point at which the pinnules originate, decreases only slightly towards the tip of the filament, and approximates to the length of the copepod's antenna excluding the three terminal claws, which are hitched over the low ridge formed by the posteriorly prolonged bases of the pinnules (Fig. 1 a). The slight lateral convexity of the filament is no hindrance to the maintanence of a secure grip, due to the above-mentioned geniculate bend in each antenna, which allows for the angle of curvature. Once a filament has been embraced in this way, and the terminal claws have attained a hold between the bases of the pinnules, the copepod is literally locked to its host.

A grappling device of such efficiency is clearly essential to a small form inhabiting the branchial fan, when one considers the lightning rapidity with which *Sabella* can withdraw into its tube. To contend successfully, however, with the current produced by so abrupt and powerful a reflex, the copepod must also be aligned in such a way that minimum resistance is offered to the surrounding water. That the position normally adopted (with the head pointing to the filament's base) achieves this object, is suggested not only by the marked antero-posterior stream-lining of the body, but also by the posture of the copepod while *in situ*.

When in position, *Sabelliphilus* rests the proximal part of the ventrally recurved rostrum on the abfrontal surface of the filament. The extreme distal portion, which is sharply bifid, is closely applied to the underside of the cephalothorax. Its base, therefore, represents the anterior tip of the copepod's body. On either side of this, and slightly in advance of the rostral base, are the two proximal joints of the antennules. These two antennular segments are considerably expanded to form flattened plates (Fig. 1 b), and since their anterior margins are in close apposition to the ventro-lateral surface of the filament, they form, along with the rostral base, a smoothly sloping shield which deflects the " withdrawal current " past the flanks and over the back of the copepod. The remaining segments of the antennule are of normal proportions and overlie the grapnel-like antennae (Fig. 1 a).

The extension of the smooth streamline initiated in this way by the anterior region, is ensured by the exaggerated flexure of all four pairs of swimming limbs. By bending the terminal joint of each leg backwards until its main axis is parallel to the ventral body surface, the copepod, as it were, " kneels "

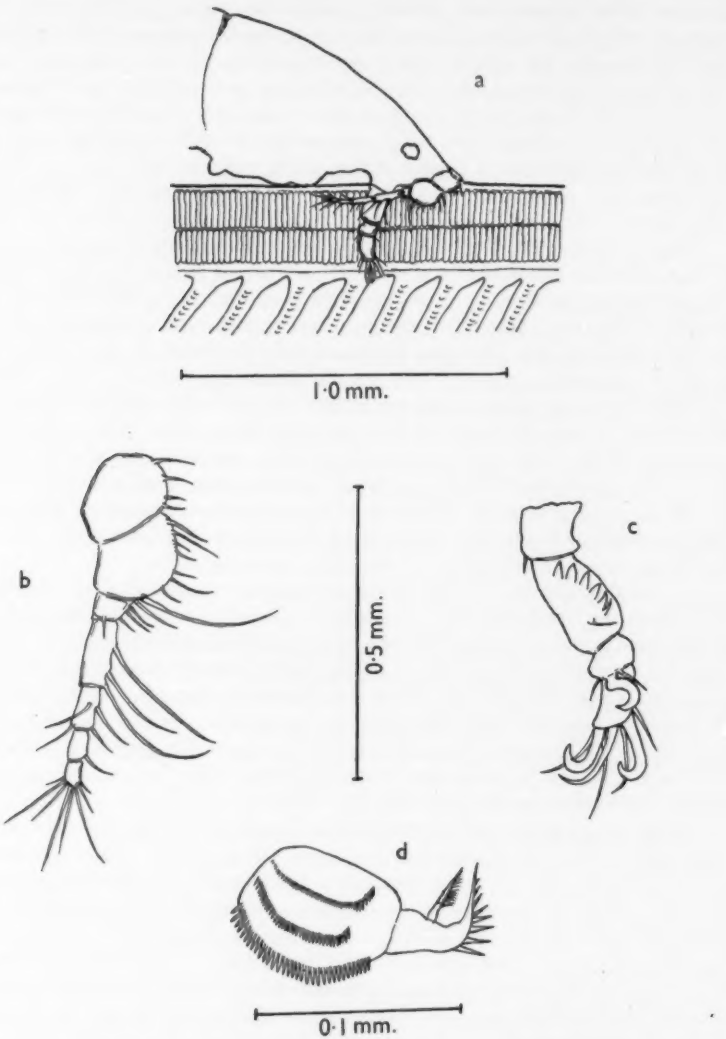

Fig. 1.—(a) Lateral view of the cephalothoracic region of a female *Sabelliphilus elongatus* on a branchial filament of *Sabella*, to show the relative positions of antennules and antennae, with the terminal claws of the latter engaged at the base of a pinnule.

(b) Antennule of female *S. elongatus*.

(c) Antenna of *S. elongatus*, medial aspect.

(d) Maxilla of *S. elongatus*.

upon the filament, thus reducing the dorsal bulge created by the posterior thoracic segments. The entire attitude, in short, is inescapably reminiscent of a profound Oriental obeisance (Plate 1, fig. 2).

Aligned in this manner, *Sabelliphilus* is admirably positioned to withstand the violent withdrawal reflex of its host. In ovigerous females the two long egg-sacs stream out posteriorly on either side of the urosome, and are towed smoothly into the host's tube when the worm retracts its branchial crown. Were the copepod to cling to the filament the other way round, these ovisacs might easily be damaged, or even sheared off, on entering the mouth of the tube.

Provided they are undisturbed, the copepods remain nearly motionless for long periods. Indeed, individuals may be recognised over several days solely by their location, which remains unaltered despite the movements of the branchial crown. It might be thought that the crowding together of the filaments when the fan is withdrawn would encourage, or at least facilitate, a change of anchorage, but this appears to happen only rarely. Direct observation of infected worms living in glass tubes confirms this continued quiescence of *Sabelliphilus* during the time its host is withdrawn.

Two movements occasionally punctuate these long spells of immobility. Firstly, the urosome may be jerked up and down several times in quick succession. This sometimes happens when a bright light is shone on the copepod, but its significance is difficult to assess. The second consists of a longer or shorter run along the filament's abfrontal surface. Since these runs are rapid and their occurrence unpredictable, it is not easy to analyse the movements involved, although the driving force would appear to be supplied by the flexed thoracic limbs. The strong exopodal spines of the terminal joints momentarily press against the filament ; simultaneously, the antennae release their hold as the copepod lunges forward, but re-engage further along before the next push is given by the legs. It seems probable that this form of locomotion explains the development of the five (or sometimes six) very powerful, backwardly directed teeth on the second joint of the antenna. Pressing into the filament on either side, they could serve to stabilize the copepod at the conclusion of its forward lunge, or even supplement the impetus derived from the thoracic limbs. If, during a run on a severed filament, the copepod " overshoots " at the cut end, it will turn extremely quickly and run back the other way.

One other noteworthy feature concerns the distribution of copepods on the branchial crown. As Nicol (1931) has pointed out, the maximum degree of expansion of the crown varies with the individual worm. Thus, in some, the two halves of the fan are drawn apart until an almost flat plate is formed, while in others a wide and shallow funnel surrounds the mouth. Especially in medium sized and large specimens there may be an area where the last dozen or so ventral filaments of one half are overlapped by the corresponding filaments of the other side. This overlap, of course, increases as the fan is rolled up during withdrawal. There is often a distinct tendency, in worms which show this feature, for the overlapped filaments to be infested by *Sabelliphilus*. Thus a remarkably high proportion of the worm's copepod population may be concentrated on this relatively small number of filaments, which represent

perhaps only one-sixth of *Sabella's* total complement. It is difficult to say why this should be so, unless one assumes that such filaments stand a greater chance of being infected in the first place. It may be that the feebly-swimming copepodites, on entering the branchial funnel, are deflected by a local current of fractionally greater strength into this particular area. Nicol (*loc. cit.*, p. 562) has stressed the considerable force of the ciliary rejection current on the lateral lips, and since the filaments involved are those towards which this current mainly flows, it is at least possible that this is the mechanism responsible. The respiratory currents studied by Wells (1951), which enter and leave the mouth of the tube, could also be considered as agents in this connection. The reluctance displayed by *Sabelliphilus* to alter its position when once established on a particular filament would then confer permanence to this uneven pattern of distribution.

THE MECHANISM OF ORIENTATION

Thus far we have been concerned mainly with the topographical relationship between *Sabelliphilus* and its host. The question remains as to how this very precise orientation is achieved by the copepod. Throughout the greater part of its length, the filament would seem to offer few clues of a purely structural nature which might assist the crustacean in aligning itself with its head towards the proximal end. It is true that the pinnules are habitually inclined at a slight angle so that their tips point away from the body of the worm, but this effect is barely distinguishable at their points of origin, which are the only portions even remotely in contact with *Sabelliphilus*. In the absence of such structural information, there can be little doubt that correct alignment depends rather on a signpost of physiological type, of which the most obvious is the ciliary activity of the host.

Nicol has described clearly the various currents produced by *Sabella* during feeding. Briefly, the abfrontal, latero-frontal and frontal cilia of the pinnules beat in such a way that a stream of water is drawn between the outspread filaments into the branchial funnel. The particles suspended in this stream are carried first to the bases of the pinnules and are then swept down the longitudinal groove on the filament's frontal surface towards the worm's mouth. As far as these collecting currents are concerned, therefore, the copepods (situated abfrontally) are exposed only to that entering the branchial funnel, which flows evenly past them on either side. Likewise, the rejection currents, transporting waste material mainly to the palps, are, with one notable exception, remote from the site occupied by *Sabelliphilus*. The exception is a current described by Nicol (p. 562) as follows : " In a certain number of worms another rejection tract can be seen. This is situated at the sides of each filament. Particles are carried by it from the basal regions of the filaments to the tips. In no case have the cilia been seen in sections, but in certain worms a flickering can be seen over the surface of the filament while particles move rapidly and steadily upwards. In other specimens no trace of this current can be found."

The examination of many filaments under high power and with careful focusing leads me to believe that such a tract is, in fact, always present, though by no means easy to demonstrate. It will be seen (Fig. 1 a) that this ciliated

path is spanned not only by the antennae of *Sabelliphilus* but also by the long setae arising from the antennular segments. A tract of this sort, with its unidirectional ciliary action in close proximity to the sensory equipment of the copepod, very probably provides the latter with sufficient information to achieve a correct alignment.

That *S. elongatus* does not apparently rely on the total pattern of ciliary currents created by an intact worm, can be shown by releasing a number of copepods into a small dish containing several freshly severed filaments arranged at random. The cilia of such filaments will continue to beat actively for some time, with the exception of most of the latero-frontals. In a high percentage of cases the copepods will still orientate correctly, with the head towards the cut base.

An interesting corollary to this experiment concerns the tenacity with which a filament is grasped. A gentle prodding of the copepod has little or no effect. Similarly, a stream of water can be pipetted towards an infected, severed filament, or the latter can even be sucked violently into and out of a pipette, without causing the copepod to release its hold. A more effective method of dislodgment is to rock the dish containing the filaments so that the whole mass of water is in movement. This disturbance, of a type not presumably experienced often in nature, usually causes a good proportion of the copepods to leave the filaments and swim rapidly away. These facts provide further evidence for the possession by *Sabelliphilus* of a finely discriminative rheotactic response, closely adapted to the structure and normal movements of its host.

FEEDING

When a comparatively active copepod is associated with the food-gathering organ of a filter-feeding invertebrate, it is perhaps natural to assume that it is living as a commensal. This does not, however, seem to be the case with *S. elongatus*. Although the evidence is mainly indirect, it points strongly to the conclusion that *Sabelliphilus* is a truly parasitic form, relying for its food on the actual substance of the fan-worm. Fryer (1957) has lately drawn attention to the attacking of large prey by carnivorous cyclopoids, and emphasized the ease with which such a habit could develop into parasitism. As we have seen, *Sabelliphilus* is not in contact with any of the food-gathering tracts along which particles pass to the mouth of the worm, nor does it make excursions to these areas. Furthermore, although it lies athwart a small rejection tract, none of the particles moving along this have been seen to be engulfed. There is, moreover, no trace of any subsidiary current created by the copepod which might deflect food particles for its own use from those entering the branchial funnel.

Perhaps the most convincing evidence for parasitic status is supplied by the results of experiments in which food is denied to the host. An infected worm, carefully taken from its tube, was placed in 500 ml of sea water from which particulate matter had been removed by passing it through a Buchner funnel with a grade 5 sinter glass filter (pore size less than two microns). 2·5 ml of penicillin and 2·5 ml of streptomycin were added to discourage bacteria, which might have constituted a source of food. Certainly the addition of these

antibiotics resulted in the water remaining remarkably clear as compared with the same quantity of untreated water. After leaving the worm for forty-seven hours until the gut had emptied, it was transferred to a clean dish containing water similarly prepared. Copepods isolated from their host were also placed in vessels with filtered or unfiltered water, and with or without antibiotics. The great majority of these isolated specimens died within eight days, whereas many of those allowed to remain on the worm lived as long as the experiment was continued—i.e. for periods of a fortnight. This would certainly seem to indicate that the copepods' source of nourishment resides in the host itself.

What substances, then, are utilised as food, and how does *Sabelliphilus* obtain them? The mouthparts of *Sabelliphilus* do not, at first sight, suggest that this copepod is adequately equipped to extract nutritive substances from the branchial filaments. As we have seen, however, the antennal armature is particularly formidable, and is moreover in continuous contact with the epithelial tissue of the host. It is sometimes noticeable that this tissue, in small areas immediately adjacent to the antennae, appears to be slightly eroded. An intensification of this effect has been observed on a worm kept under somewhat unhealthy conditions, when the epithelium was raised into a small gall-like swelling just in front of the sharp anterior edges of the proximal antennular segments. In addition, the armature of the maxilla is rather more complex than that figured by Sars, and I have, therefore, redrawn it (Fig. 1 d). As well as the single row of stout spines described by the Norwegian author, two anterior rows of smaller spines are also present which likewise lie in close apposition to the surface of the filament. The abrasive actions here ascribed to these two appendages have not, it is true, been witnessed, but this may well be due to the difficulty of observing copepods on an intact worm under natural conditions, with an objective of sufficient power to reveal their detailed movements. It is, however, clear that *Sabelliphilus* does in fact possess tools potentially capable of damaging the epithelial tissue.

The gut contents appear as a rust-brown mass, the colour matching almost perfectly the carotenoid pigments of the worm's fan. No remains of small organisms have been seen. Close examination reveals that the coloration is due to the presence of minute brownish-red particles, often arranged in groups. In the rectal region the whole mass becomes more compact and the colour darkens as the faecal pellet is formed. Here and there throughout the alimentary canal globules of fat or oil are also apparent.

The extensive distribution of carotenoid pigment on the branchial filaments implies the equally wide occurrence of the oily or fatty substances normally associated with this pigment. It seems probable that puncture or erosion of the superficial tissue would expose these products for utilisation by *Sabelliphilus*, which would also incidentally engulf numerous pigment granules. There is, indeed, some evidence (albeit inconclusive) that the copepods on occasion show a preference for remaining on the small heavily pigmented bands which occur at regular intervals along sabellid filaments. It is also perhaps significant that the basal regions of the pinnules, in which the antennal claws engage, are extremely rich in mucus cells, and strands of mucus can

frequently be seen clinging to the copepods' appendages. A possible source of protein is thus readily available, the production of which might well be stimulated by contact with the antennal armature.

Finally, as regards the genesis of this association, it is not difficult to visualise ancestral habits of predation, perhaps on a wide range of invertebrates, gradually becoming transformed as attention is increasingly focused on sabellid worms. The copepod, once committed to this source of food, would then be selectively moulded still further into its present status of a specialised ectoparasite. The fact that even heavily infected worms appear to remain healthy indicates that a considerable degree of stability has been achieved in this association.

SUMMARY

A detailed account is given of the alignment, attitude and behaviour of the cyclopoid copepod *Sabelliphilus elongatus* on the branchial filaments of the polychaet *Sabella pavonina*.

It is thought that the direction of alignment is governed by the withdrawal reaction of the host, both orientation and posture being designed to avoid dislodgment from the fan during this movement.

The copepod appears to rely for correct orientation on its sensitivity to the ciliary action of a small rejection tract on the filament's abfrontal surface.

Evidence is presented for regarding *S. elongatus* as an ectoparasite which extracts oil or fat by slight erosion of the pigmented epithelium, and which may also utilise mucus. Cells producing the latter substance are possibly stimulated through contact with the parasite's antennal claws.

ACKNOWLEDGMENTS

My thanks are due to Professor R. A. R. Gresson for the provision of research facilities ; to Dr Denis L. Fox, Scripps Institute, California, for helpful correspondence ; to Messrs S. Armstrong and W. Ferguson for photographic assistance ; and to Gwyneth Gotto, B.Sc., for discussion and criticism. I am also indebted to Dr. J. P. Harding for reading the manuscript.

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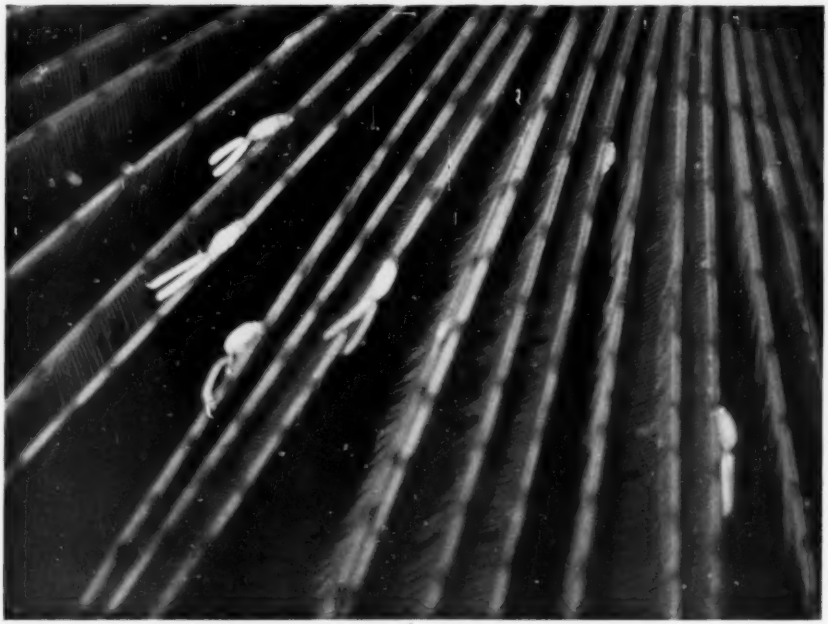

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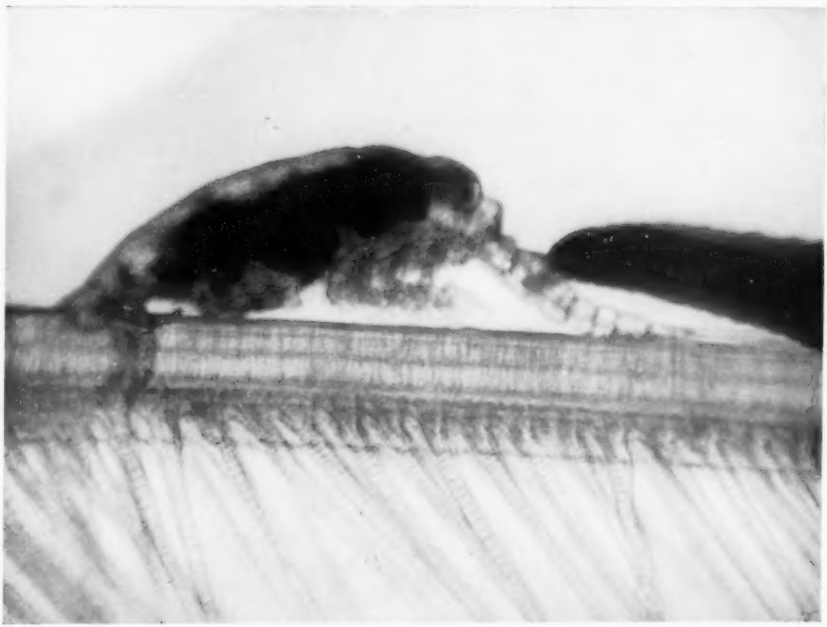

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1.—Part of the branchial crown of *Sabella*, with five ovigerous females and one immature stage of *Sabelliphilus elongatus* clinging to the abfrontal surface of the filaments, and all orientated towards the base of the crown.

2.—Ovigerous female of *S. elongatus* on a branchial filament, showing the marked flexure of the thoracic limbs. The copepod is about 1·7 mm. in length.

STUDIES ON SOME PARASITIC CRUSTACEANS ON AFRICAN FRESHWATER FISHES, WITH DESCRIPTIONS OF A NEW COPEPOD OF THE GENUS *ERGASILUS* AND A NEW BRANCHIURAN OF THE GENUS *CHONOPELTIS*

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(With 26 figures in the text)

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INTRODUCTION

The aim of the present paper is to describe two new crustacean parasites of African freshwater fishes, to present some miscellaneous items of information on the biology and taxonomy of the African freshwater parastic Copepoda and Branchiura, and to place on record a number of distribution records of various species. The latter will be utilised in a subsequent paper dealing with the distribution patterns of these organisms.

A NEW COPEPOD OF THE GENUS *ERGASILUS* FROM LAKE RUDOLF

The species described below was found on the gills of two species of *Tilapia* from L. Rudolf in the collection of the East African Fisheries Research Organisation.

ERGASILUS LATUS sp. n. (Figs. 1–6)

Adult female

Length to about 900 μ. Cephalothorax fused to somite of leg 1, longer than wide, bluntly rounded anteriorly, somewhat bulged laterally, and shallowly indented in posterior third. Dorsal chitinous frame in form of an inverted T. No other head sculpture detected.
Somites of legs 2–5 distinct.

Abdomen of three somites. Genital somite wider than long and gently bulged laterally so as to be widest in middle. Last two abdominal somites very short. Furcal rami simple, a trifle longer than wide and armed with five terminal setae of which innermost is by far the longest and stoutest. Longest furcal seta with characteristic bend near its proximal end.

Antennule of six segments. Antenna prehensile, long and slender and of form shown in Figs. 1 and 2.

Legs 1–4 of structure typical for genus, having following arrangement of spines and setae.

P1	Exopod	0–0	1–1	2–5
	Endopod	0–1	0–1	2–4
P2	Exopod	0–0	0–1	0–6
	Endopod	0–1	0–2	1–4
P3	Exopod	0–0	0–1	0–6
	Endopod	0–1	0–2	1–4
P4	Exopod	1–0	0–5	
	Endopod	0–1	0–2	1–3

Leg 5 very broad ; armed with two terminal setae almost as long as leg itself, and one shorter lateral seta.

Egg sacs fairly long—reaching beyond end of longest furcal seta.

Colour (preserved specimens) faint brown with traces of purple pigment ventrally in cephalothorax.

Hosts

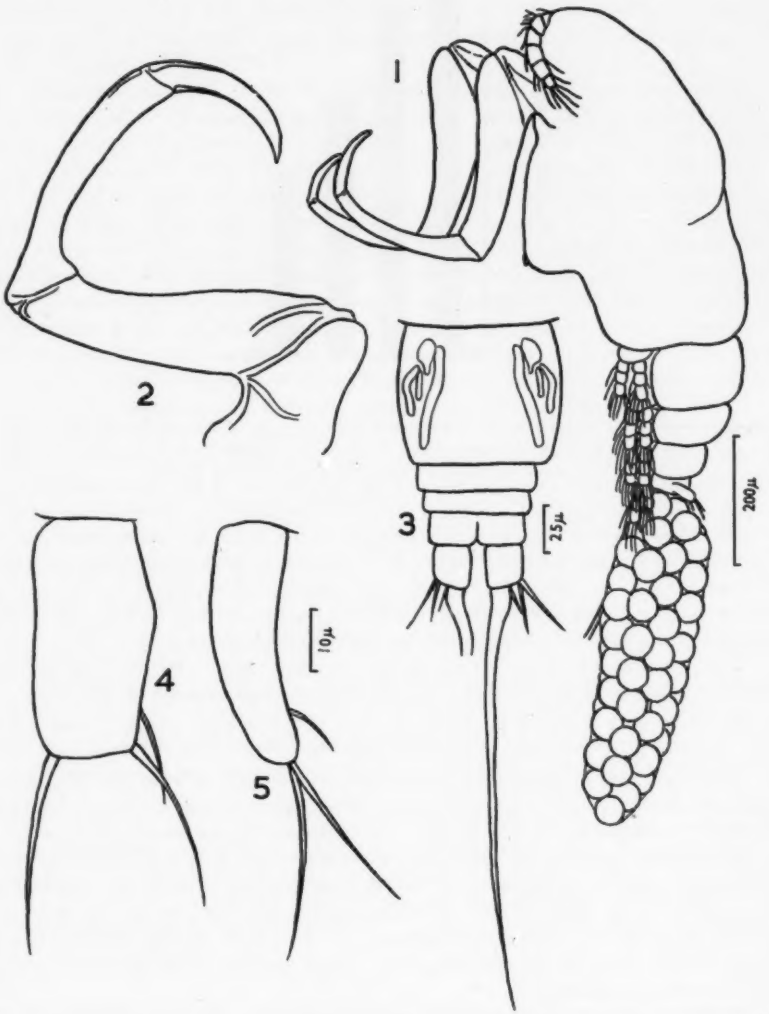
Tilapia nilotica (L.) and *T. galilaea* (Artédi)

Distribution on host

In all four of the infected hosts the parasites were located approximately half way along the gill filament and showed a marked preference for the outer (anterior) face of the gills and a somewhat less marked, though quite distinct, preference for the more anterior sets of gills. This is most clearly demonstrated by a histogram (Fig. 6).

Affinities

The somewhat swollen region near the joint between segments 2 and 3 of the antenna is reminiscent of the condition found in *E. nodosus* Wilson, a species collected from *Bagrus bayad* (Forskal) in the P. Nile (Wilson, 1924) to which *E. latus* appears to be closely related. In *E. latus*, however, this swelling is less conspicuous than in *E. nodosus* and, although some of the



Figs. 1—5. *Ergasilus latus* sp. n. 1. Adult ♀ lateral. 2. Antenna. 3. Genital somite abdomen and furcal rami, dorsal. 4. Leg 5, dorsal. 5. Leg 5, lateral.

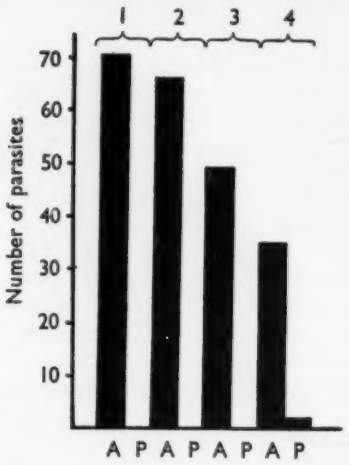


Fig. 6.—Distribution of individuals of *Ergasilus latus* on gills of four specimens of *Tilapia*. Numbers 1–4 refer to the sets of gill filaments numbered from anterior to posterior. A= Anterior face ; B=Posterior face of gill filaments.

characteristics listed for *E. nodosus*, such as the complete absence of leg 5, can only be accepted with reserve, *E. latus* has several other characteristics which indicate its distinctness from this species. For example, the fusion of the somite of leg 1 with the cephalothorax, the six-segmented antennule, and the quite different arrangement of the furcal setae.

The very broad leg 5, to which the specific epithet refers, enables this species to be readily separated from all other African species of *Ergasilus*.

NOTES ON *ARGULUS RHIPIDIOPHORUS* Monod

Nothing appears to have been recorded concerning *Argulus rhipidiophorus* since its description by Monod (1931), whose material came from L. Albert. Recently I obtained several examples from preserved specimens of the catfish *Clarias lazera* Cuvier and Valenciennes, collected in L. Rudolf by Mr D. J. Garrod, and have located others in the British Museum collections (where they languished under the label *A. africanus*) which had been collected in L. No on the upper White Nile (one specimen), L. Naivasha, Kenya (several specimens) and L. Rudolf (three specimens). Host data are lacking in the case of all the museum specimens.

Study of these specimens plus some from the original collection from L. Albert kindly sent to me by Mr P. L. G. Benoit, revealed a certain amount of variation which is discussed below.

The lateral spine of the antennule is variable in size but is usually quite small.

The armature of the antennae consists of pointed spines. These are usually sharply pointed (Figs. 15 and 16) but in some of the L. Rudolf specimens

(Fig. 8) the spines are relatively short. Variation is also shown by the natatory lobe of leg four. In extreme cases from L. Rudolf this lobe is very short (Fig. 12), in material from L. Albert it is more attenuated (Monod's Fig. 20 a), and in the L. No and L. Naivasha specimens it is even more attenuated and is scarcely to be separated from its counterpart in *A. africanus* Thiele with which comparison is made below.

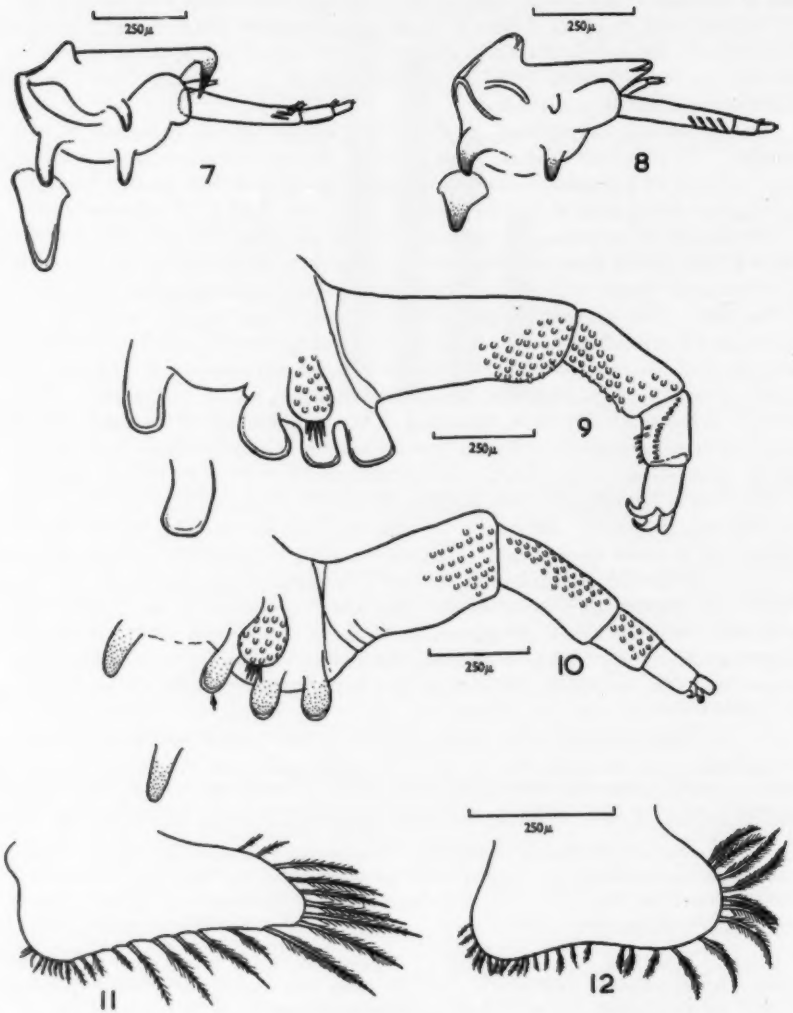
The deposition of pigment on the dorsal surface of the carapace is also variable. The extreme forms, again from L. Rudolf, have relatively few but large clumps of pigment. Other specimens have more but smaller clumps, the pattern being similar but less broken than that seen in *A. africanus*.

Monod draws attention to the similarity of *A. rhipidiophorus* and *A. reticulatus* Wilson, but does not refer to the likeness of the former to *A. africanus* to which it is closely related and with which it has apparently been confused in the past. The similarities are in fact so marked that a good case could be made out for regarding *A. rhipidiophorus* as a subspecies or, now that we know something of the range of variation of one well defined species—*A. brachypeltis* Fryer (Fryer, 1959)—even as an extreme variant of *A. africanus*. Most striking is the similarity in the structure of the modified legs of the males which are usually diagnostic of different species among the Branchiura but which, apart from slight and perhaps not even constant differences in the natatory lobes of leg 4 are not definably different in the two species. In spite of this remarkable similarity, the males of the two species can be separated by differences in other appendages. The most satisfactory method of comparison is by means of illustrations, and to this end certain appendages of the two species are illustrated side by side. This also has the advantage of making available illustrations of *A. africanus* which is a common and widespread species in Africa, but of which descriptions and figures are by no means readily accessible. The salient features of these comparisons are outlined below.

A. africanus	*A. rhipidiophorus*
No anterior hook on antennule. (Fig. 7)	Anterior hook present on antennule. (Fig. 8)
Spines of antennule and antenna broad and spatulate and clear light brown in colour. (Fig. 7)	Spines of antennule and antenna rather pointed, dark, brown, and heavily scleratized (Figs. 8, 15 and 16).
Spines of maxilla very broad and spatulate and the three on seg. 2 close togther. (Fig. 9)	Spines of maxilla less broad, more rounded and widely separated. (Fig. 10)
Natatory lobe of leg four of drawn out into an elongate and tapering lobe. (Fig. 11)	Natatory lobe of leg 4 of sometimes scarcely drawn out and broadly rounded. (Note : Fig. 12 represents an extreme case)
Carapace of female with pigment deposited in numerous small clumps. (Fig. 13)	Carapace of female with pigment deposited in fewer large clumps. (Fig. 14 represents an extreme case)

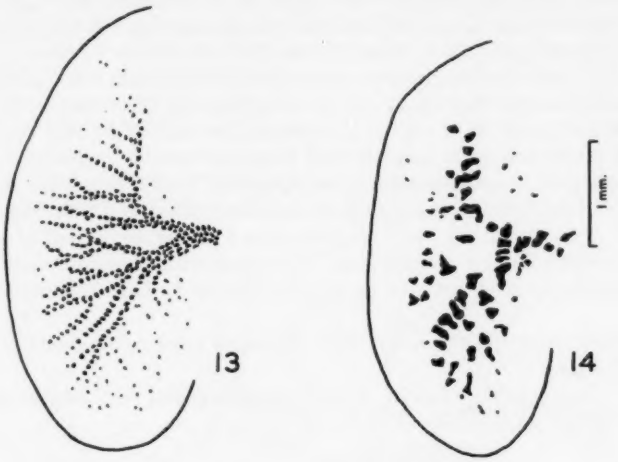
In addition, large specimens of *A. africanus* have an abdomen which is longer than wide, but in similar sized specimens of *A. rhipidiophorus* the abdomen is wider than long.

The decision to refrain from altering the status of *A. rhidiophorus*, at least for the time being, is based in part on geographical grounds (including ignorance of the full range of *A. rhipidiophorus*) and in part on the knowledge that



Figs. 7–12.—Comparison between *Argulus africanus* Thiele and *A. rhipidiophorus* Monod. 7. Antennule and antenna of *A. africanus*. 8. The same of *A. rhipidiophorus* from L. Rudolf. 9. Maxilla of *A. africanus*. 10. Maxilla of *A. rhipidiophorus*. 11. Natatory lobe of leg 4 of ♀ of *A. africanus*. 12. The same of *A. rhipidiophorus*. (Note : In Fig. 10, the spine indicated by an arrow was drawn from the corresponding structure on the other side as in the appendage illustrated it was deformed.)

specimens of *A. africanus* from such widely separated localities as Lakes Nyasa, Bangweulu and Victoria are very constant in form.



Figs. 13–16.—Comparison between *Argulus africanus* and *A. rhipidiophorus* and further details of *A. rhipidiophorus*. 13. Pattern of pigmentation of left lobe of thoracic portion of carapace of *A. africanus*, ♀, dorsal. 14. The same of *A. rhipidiophorus*. Extreme type from L. Rudolf. 15. Innermost spine of antenna and mesial spine of a specimen of *A. rhipidiophorus* from L. No. 16. The same from a specimen from L. Naivasha.

THE TRUE MALE OF *Argulus ambloplites* Wilson, AND A REAPPRAISAL OF THE STATUS OF *A. jollymani* Fryer

In 1920 C. B. Wilson received from the Dungu River, one of the north-eastern tributaries of the Congo, two branchiurans which he took to be the male and female of a single species, and he accordingly described them as such, giving them the name *Argulus ambloplites*. Doubts were cast on the

correctness of this procedure by the finding of a new species *A. jollymani* Fryer in Lake Nyasa whose females were very similar to those of *A. ambloplites* described by Wilson, but whose males differed markedly (Fryer, 1956). Shortly afterwards I received from the late Mr P. I. R. Maclaren five specimens of *A. ambloplites* which he had collected from a specimen of *Clarias mossambicus* Peters in Mulungushi Dam, near Broken Hill, Northern Rhodesia. One of these was a male and its structure proves conclusively that the male described by Wilson does not belong to the same species as the female. As Wilson described the female first it is to the species represented by this sex that the name *A. ambloplites* must be given and the male must be re-named.

The male of *A. ambloplites* can be described briefly as follows. Length to 7·0 mm. General form similar to that of female. Carapace 1·24 times as long as wide. Posterior lobes reaching back so as to cover about half of abdomen, and converging but not overlapping. Carapace with numerous dark pigment spots dorsally as described and figured for a female from L. Bangweulu (Fryer, 1959).

Abdomen very slightly longer than wide and comprising about 21 per cent of total length.

Leg 1 as in female. Legs 2, 3 and 4 modified and very similar in form to those of *A. jollymani* (Fig. 59 in Fryer, 1956).

Remarks

The male of *Argulus ambloplites* is very similar indeed to that of *A. jollymani*, even in the structure of the copulatory apparatus of the legs which is usually a diagnostic characteristic of different Argulids. (But see notes on *A. rhipidiophorus* and *A. africanus* in this paper, p. 633). The only real structural difference between these forms lies in the structure of the supporting rods of the suckers. In *A. ambloplites* the rods consist of very few pieces (Wilson, 1920, Fryer, 1959) while in *A. jollymani* the pieces are more numerous (Fryer, 1956). In addition, specimens of *A. ambloplites* from both L. Bangweulu and Mulungushi Dam were distinctly spotted dorsally, while no such spots were present in *A. jollymani* from L. Nyasa. *A. jollymani* also occurred under more open-water conditions than did *A. ambloplites*.

It thus seems reasonable to regard *A. jollymani* as a sub-species of *A. ambloplites* which is beginning to diverge both structurally and ecologically from the parent form in the open waters of L. Nyasa. This form should therefore henceforth be known as *Argulus ambloplites jollymani*.

It is interesting to note that it is the supporting rods of the suckers which are diverging in form in the two sub-species. This may be an adaptive change which facilitates attachment to different hosts under different conditions of life.

NOTES ON *ARGULUS DARTEVELLEI* BRIAN AND A DESCRIPTION OF THE MALE

While it seems probable that *A. dartevellei* Brian is more truly a marine than a freshwater species the present note is justified by the fact that, although the three specimens which I recently collected were taken from a fish which had probably just run up from the sea, they were indeed collected in a truly freshwater habitat.

Formerly only a single female specimen of this species was known. This was taken from a specimen of *Polynemus quadrifilis* Cuvier and Valenciennes by the late Dr E. Dartevelle near the mouth of the Congo (Brian, 1940). I found two males and a female on a large specimen of *Promicrops distalis* Roux and Calligan captured in the R. Kouilou in French Equatorial Africa about half a mile from the sea, in water which was quite fresh. Dr Roux informs me that *P. distalis* is a marine fish which enters rivers at certain times of the year.

My female specimen had a length of 8·00 mm. as compared with about 5·5 mm. in the holotype, and differed from it in that the carapace did not extend sufficiently far back to cover the fourth pair of legs. Such changes of carapace length in relation to size are known in other species, for example *A. brachypeltis* Fryer. Otherwise it exhibited all the characteristics described by Brian.

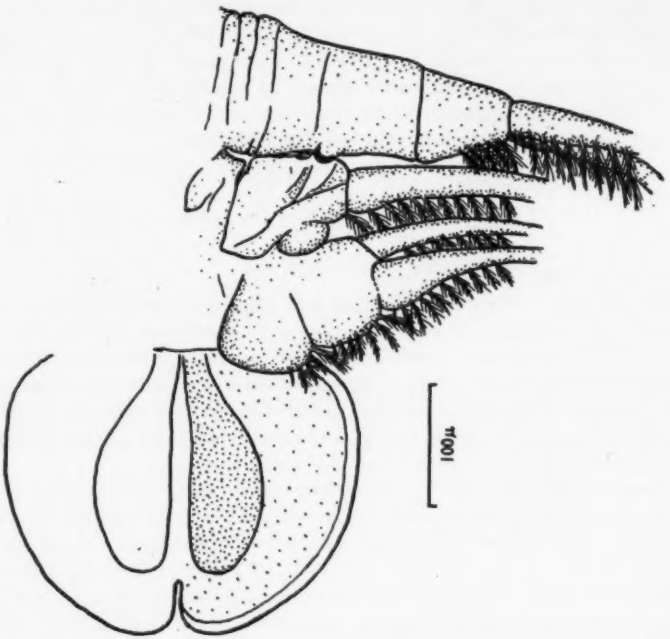


Fig. 17.—Legs, 2, 3 and 4 and abdomen of *A. dartevellei* Brian, ♂, ventral.

The colour of the living specimen was a rather greyish white, tending to brownish. The male can be described as follows :—

Adult male

Length to 7·2 mm.

General form like that of female. Carapace very slightly longer than wide (about 1·05 and 1·07 times as long as wide in available specimens), and extending

backwards to cover the fourth pair of legs, but leaving the abdomen entirely uncovered.

Abdomen wider than long. Similar in shape to that of female but proportionately longer, being about 18 to 19 per cent of total length. (As opposed to about 11 per cent in the single female available and, so far as can be ascertained from his figure, about 14 per cent in Brian's female).

Cephalic appendages as in female. Leg 1 as in female. Legs 2, 3 and 4 modified and of structure shown in Fig. 17.

A NEW BRANCHIURAN OF THE GENUS *CHONOPELTIS* FROM THE CONGO SYSTEM

A description of the species recorded below was originally prepared from three specimens, a male and two females, collected in L. Mweru by Mr R. Kleinschmidt. Later, however, I found a single female labelled *C. inermis* var *schoutedeni* in the collection of the Musée Royal du Congo Belge which had been collected at M'Bunzi on the R. Fimi in the Lower Congo, and eight specimens on fishes collected in the Malagarasi Swamps by members of the East African Fisheries Research Organisation. It would appear, therefore, that this species is of widespread distribution within the Congo System.

CHONOPELTIS FLACCIFRONS sp. n. (Figs. 18–25)

Adult female

Length to about 7·4 mm.

Body elongate. Carapace trifoliate and short, not reaching back to base of second pair of legs, and occupying some 44 to 47 per cent of total body length. Width of anterior (cephalic) lobe of carapace a little more than half maximum carapace width. Cephalic lobe of carapace without any supporting rods of chitin (such as occur in other species of the genus) ventrally. Respiratory areas of carapace similar to those of other species of genus. Eyes very small. Ocellus minute ; located halfway along carapace.

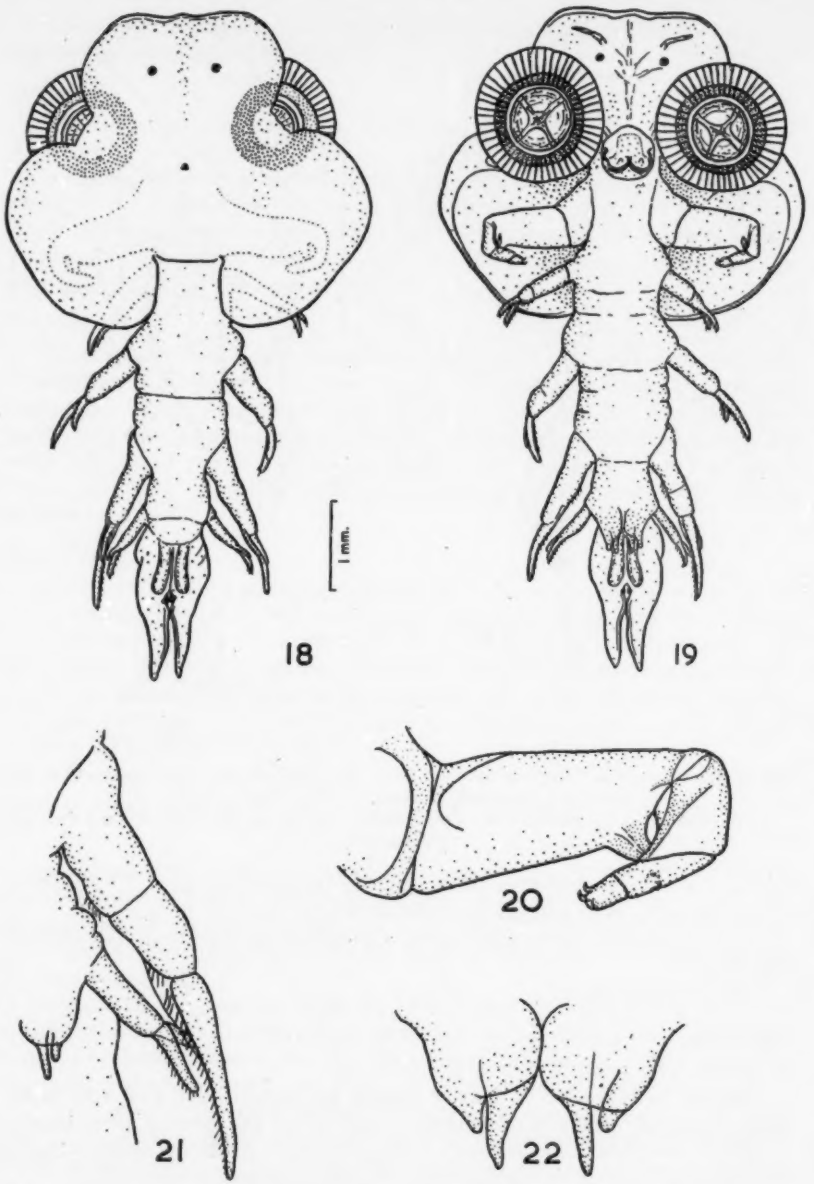
Abdomen relatively short ; comprising some 22 to 23 per cent of total body length. Furcal rami minute, situated near base of abdominal lobes.

Anterior appendages, including suckers, very similar to those of other species of genus. Sucker diameter about 35 to 36 per cent of carapace width. Maxilla rather short, of five segments. Second segment short, slightly tapering and approximately twice as long as maximum width, and with a chitinous thumb on posterior margin distally which, by apposition with the three short distal segments, converts the appendage into a prehensile structure.

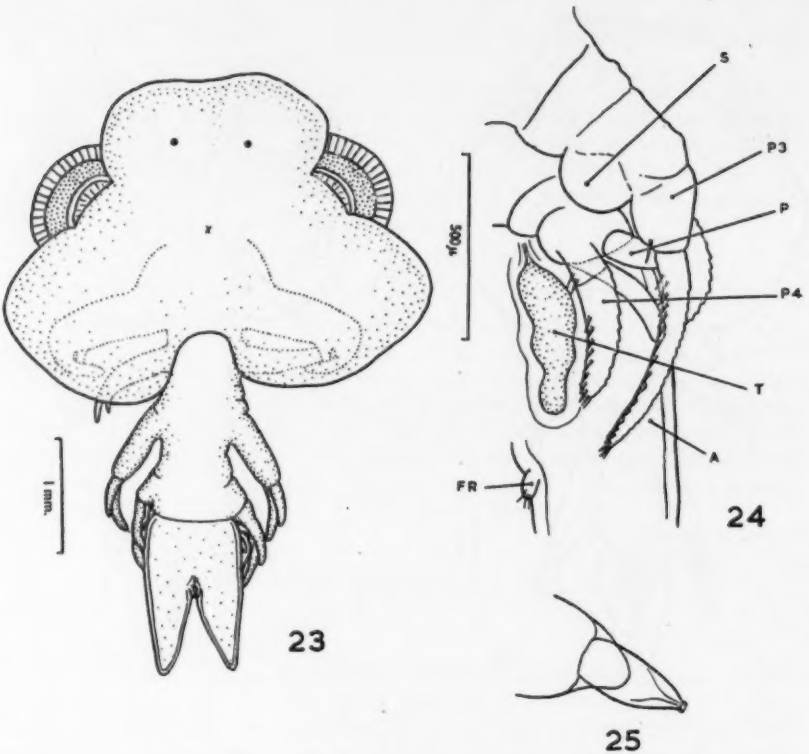
Leg 1 very small, consisting of a 2-segmented sympod with two slightly unequal rami.

Leg 2 similar to leg 1 but considerably larger.

Leg 3 basically similar to legs 1 and 2 but much more elongate and reaching back beyond extremity of leg 4 and rather more than halfway along abdomen. Rami very unequal, the ventral being approximately twice as long as the dorsal.



Figs. 18–22.—*Chonopeltis flaccifrons*, sp. n. 18. Adult ♀ (holotype), dorsal. 19. The same, ventral. 20. Maxilla. 21. Legs 3 and 4, and natatory lobe, ♀, ventral. 22. Natatory lobes of fourth pair of legs.



Figs. 23–25.—*Chonopeltis flaccifrons*, sp. nov. Male. 23. Adult, dorsal. 24. Legs 3 and 4, and associated structures, ventral. 25. Peg of leg 4, dorsal.
A—abdomen; T—testis; F.R.—furcal ramus; S—socket; P—peg; P3 and P4—legs 3 and 4.

Leg 4 similar to preceding pairs but even smaller than leg 1. "Natatory lobe" distinctly bifid and having form shown in Figs. 19, 21, and 22.

Spermathecae elongate and having a length rather less than half that of abdomen.

Colour, milky white.

Adult male

Length to 5·2 mm.

General form similar to that of female but more squat and with much wider carapace. Maximum carapace width 67–72 per cent of total length. Length of carapace 52–55 per cent of total length. Abdomen slightly longer than that of female ; comprising some 27–30 per cent of total length.

Legs 1 and 2 similar to those of female. Legs 3 and 4 modified for copulation, and having form shown in Figs. 24 & 25.

Testis sacs rather short, not extending back in abdomen as far as point reached by extremity of leg 3.

Hosts

The three specimens from L. Mweru all occurred on the mormyrid fish *Marcusenius discorhynchus* (Peters), that from the R. Fimi occurred on *M. welwerthi* Boulenger, and the specimens from the Malagarasi Swamps also occurred on *Marcusenius* sp. Both *C. schoutedeni* Brian and *C. congicus* Fryer which also occur in the Congo system also parasitize, so far as is known exclusively, members of this family. All the specimens observed *in situ* on the host occurred under the operculum.

General remarks

While distinguishable by numerous well-marked characteristics the most outstanding peculiarity of this species is the absence of any sign of chitinous supporting rods in the anterior region of the carapace, and it is from this peculiarity that the specific epithet is derived. It is readily distinguished from all other species of the genus by this feature, by the form of the so-called " natatory lobes ", and by the structure of the posterior pairs of legs in both sexes.

Affinities

The possession of a prehensile maxilla of *C. flaccifrons* indicates that it is more closely related to *C. schoutedeni* than to any other species of the genus, for these two species are the only ones which exhibit such modification of this appendage. The elongate nature of the third pair of legs of the female supports the idea of such a relationship for these appendages approach more closely the structure exhibited by the third pair in *C. schoutedeni* than those of either *C. inermis* Thiele or *C. congicus*.

NOTES ON THE SPECIMENS OF *CHONOPELTIS* RECORDED FROM THE UELÉ AND OKAVANGO RIVERS

Specimens of *Chonopeltis* whose identity was given as *C. inermis* have been recorded from the Uelé River (Congo system) by Monod (1928) and from the Okavango River (Zambezi system) by Barnard (1955). Through the courtesy of the Musée Royal du Congo Belge and Dr K. H. Barnard I have been able to see these specimens.

Only one female specimen from the Uelé appears to survive, and this is in very bad condition. It differs from all the many *C. inermis* I have seen from L. Nyasa in that the carapace is both relatively and absolutely longer. Monod, who figured the same specimen, shows the lobes reaching back so as to cover the second pair of legs, but now they partially cover even the bases of the third pair. This may be due in part to the method of preservation as the holotype of *C. inermis* from L. Nyasa is figured by Thiele (1904) as having a slightly longer carapace than any of the specimens found later in the same lake. However, this seems to be at most only partially responsible for the state of the specimen under review.

In addition the eyes are slightly larger than in the Nyasan material, and on one side the spermatheca extends further into the abdominal lobe than is typical of *C. inermis*. The other side is distorted.

The appendages appear to be the same as in *C. inermis* but are not in a sufficiently good condition to examine in detail. The suckers are badly shrunk.

So far as can be ascertained therefore it would appear that this specimen shows differences from *C. inermis* which are sufficient to merit at least subspecific distinctness, but until more material is forthcoming it seems unwise to make a definite pronouncement.

Examination of the juvenile specimens from the Okavango River has shown that until more is known of the juvenile stages of the various species it will not be possible to name them with certainty. They are very similar to adult *C. inermis* but differ in having a less elongate and more clearly segmented thorax, a less elongate abdomen, and in having the furcal rami located nearer to the posterior end of the abdominal lobes. Whether these are specific or merely juvenile characteristics is not yet known.

KEYS TO THE SPECIES OF *CHONOPELTIS*

Four species of *Chonopeltis* have now been described from the inland waters of Africa. In addition the literature contains references to "*Chonopeltis japonicus*" from Japan. After a fruitless search for information on this species I was informed by Dr V. Brehm that the name was originally printed inadvertently instead of *Argulus japonicus!* The genus *Chonopeltis*, therefore, is known only from Africa. The following keys will enable the various species to be identified*

Females

1 (2)	Maxillae prehensile	3
2 (1)	Maxillae not prehensile	5
3 (4)	Abdominal lobes very long ; distinctly more than one-third of total body length. Leg 3 very large and curved like a scimitar	*C. schoutedeni*
4 (3)	Abdominal lobes short ; much less than one-third of total body length. Leg 3 long and slender ; not curved like a scimitar.....	*C. flaccifrons*
5 (6)	Leg 4 minute, often difficult to see and not projecting from body. Abdominal lobes short ; equal to about half maximum width of caparace.....	*C. congicus*
6 (5)	Leg 4 not minute, always readily seen, and projecting from body. Abdominal lobes more than half maximum width of carapace....	*C. inermis*

* Since these keys were prepared, a further species of *Chonopeltis* has been discovered in the Victoria Nile. Some time will of necessity elapse before this species can be described. Meanwhile the above keys will enable the species hitherto known from the Congo and Zambezi systems to be identified.

Males

1 (2)	Maxillae prehensile	3
2 (1)	Maxillae not prehensile	5
3 (4)	Abdominal lobes long and slender. Leg 3 extending only about half way along testis	*C. schoutedeni*
4 (3)	Abdominal lobes very short. Leg 3 reaching beyond end of testis	*C. flaccifrons*
5 (6)	Leg 2 with a broad roughened plate posteriorly. 'Peg' of leg 4 conical	*C. congicus*
6 (5)	Leg 2 with two simple roughened pegs posteriorly. 'Peg' of leg 4 cylindrical	*C. inermis*

DISTRIBUTION RECORDS

The distribution patterns of the crustacean parasites of African freshwater fishes are of considerable interest and I hope to discuss these in a subsequent paper. Before this can be done, however, it is desirable to collect as many new distribution records as possible. Those published here represent the results of collections made by myself and others and serve to extend our knowledge of the distribution of several species. Records confirming the occurrence of a given species in a particular body of water are not mentioned unless there are new ecological data to add. No mention is made of species recently collected in L. Victoria. The crustacean parasites of this lake are now being studied and will, it is hoped, form the subject of a separate paper in due course.

BRANCHIURA

Dolops ranarum (Stuhlmann)

River Congo. Leopoldville. I recently took a few specimens of this species from a specimen of *Ophiocephalus obscurus* Günther, offered for sale in the African market at Leopoldville, Belgian Congo. The fish had been caught in the adjacent River Congo. This appears to be the first record of this species from the Congo proper, though it has been recorded from Lakes Tanganyika, Mweru and Bangweulu, all of which ultimately drain into it.

Upper Zambezi. Several specimens were taken by the late Mr P. I. R. Maclaren from a specimen of *Clarias mossambicus* Peters in the North Kasisi (or Kashizki) River, which runs into the Upper Zambezi at Chavuma, near Balovale, N. Rhodesia.

Middle Zambezi. I found a single specimen on *Tilapia mossambica* (Peters) caught in the middle region of the Zambesi, near Chiboboma. This and the previous record appear to be the first for *D. ranarum* in the Zambezi proper, though it is known from the Nyasan area which is in the Zambezi drainage system.

Kafue River. Two specimens were taken from species of *Serranochromis*, caught near Mazabuka, by Mr D. Harding.

Fort Johnstone, L. Nyasa. A dozen specimens, collected by Dr C. Christy in 1926 are in the collections of the British Museum (Natural History). From the date on the label it is not clear whether these were collected in the lake

itself or in the Upper Shire River on which Fort Johnstone lies a few miles below the outlet of the lake. From whichever of these localities the specimens came they are of great interest in emphasising the ecological (as opposed to host) preferences of this species. Only a single specimen of *D. ranarum* was found in the open waters of the northern part of L. Nyasa during two years observations there, yet it was occasionally found on fishes from inflowing rivers of which only a small number was examined (Fryer, 1956). Conditions prevailing near the mouth of the Shire River and in the river itself are quite different from those found in the open lake and are similar to those under which this species has been found in other localities.

Lake Nabugabo, Uganda. Specimens from L. Nabugabo, which is shut off from the north western part of L. Victoria and contains a fauna obviously derived from this lake, were collected by the Cambridge University Expedition to the E. African lakes (1930) and are now in the British Museum collection. The host is not recorded.

Lake Baringo, Kenya. Specimens collected by Dr E. B. Worthington in 1930 are in the British Museum collection. The host is not recorded.

Argulus africanus Thiele

Lower Mulungushi River, N. Rhodesia. Several specimens, taken from a specimen of *Heterobranchus* sp., by the late Mr P. I. R. Maclaren, were sent to me by their collector. This river drains by way of the Lusemfwa and Luangwa Rivers into the Zambesi.

Lake Mweru. A few specimens were collected for me from *Mormyrops deliciosus* (Leach), *Heterobranchus longifilis* Cuvier and Valenciennes and *Eutropius banguelensis* Boulenger by Mr R. Kleinschmidt.

Argulus japonicus Thiele

Alexandria, Egypt. A specimen in the British Museum is labelled " from a Royal Carp, Alexandria. Fouad 1st Institute of Hydrobiology and Fisheries ".

This species, which has usually been referred to in European literature as *A. pellucidus* Wagler, appers to be acquiring a world-wide distribution by being dispersed with the Carps which it parasitizes and which are used in pond culture. This is the first record for Africa.

Chonopeltis schoutedeni Brian

Malagarasi Swamps, Tanganyika Territory. Three specimens were found on two preserved specimens of *Mormyrus* sp. collected at Iragalla by members of the East African Fisheries Research Organisation.

Lake Mweru. Two specimens of this species were collected by Mr R. Kleinschmidt from *Marcusenius discorhynchus* (Peters) in L. Mweru. As noted briefly in the re-definition of this species (Fryer, 1959) the single female specimen had somewhat longer abdominal lobes than is typical of the specimens from either the lower Congo or the nearby L. Bangweulu. Whether this variation is phenotypic or genotypic is unknown.

COPEPODA

Lernaea haplocephala (Cunnington)

Malagarasi Swamps, Tanganyika Territory. Three specimens were found on the flanks of specimens of *Polypterus congicus* Boulenger collected at Iragalla by members of the East African Fisheries Research Organisation.

Lernaea barnimiana (Hartmann)

Lake Mweru. Although *L. barnimiana* has already been recorded from L. Mweru it is worthy of note that some particularly large specimens were taken from *Tilapia macrochir* Boulenger by Mr R. Kleinschmidt. The largest had a length of 16·3 mm. which is the greatest length recorded for this species. Specimens taken from *Labeo altevelis* Peters in the same lake were smaller than those from *T. macrochir*.

Lernaea longa Harding

Lualaba River, Belgian Congo. Although the anterior portion of the body, including the anchor, is missing from two specimens of *Lernaea* now in the Congo Museum, and although in one specimen (Fig. 26) the pregenital

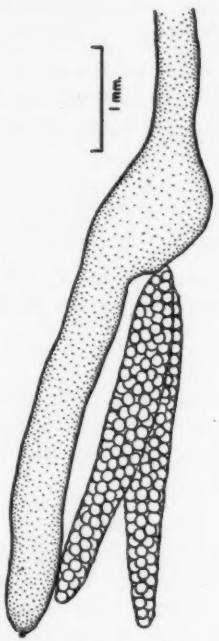


Fig. 26.—Abdominal region (somewhat atypical) of *Lernaea longa* Harding.

prominence shows stronger development than is the case in the types described by Harding (1950), I have little doubt that these should be referred to

L. longa. The abdominal region of the other specimen was very similar to that of Harding's specimens of *L. longa* which differs markedly from all other African species. In the present material the egg sacs were better developed than in the types. The Lualaba specimens were collected at Maka and occurred in the branchial cavities of specimens of *Lates niloticus* (L.). The same species, or at least a subspecies of it, served as host for Harding's material from L. Rudolf which was previously the only known locality for *L. longa*.

Afrolernaea longicollis Fryer

Middle Zambezi. I collected several specimens of this species from specimens of *Marcusenius discorhynchus* (Peters) captured in the Zambezi River near Chibobma. Notes on the morphology of these specimens and those recorded below are given elsewhere (Fryer, 1959).

Malagarasi Swamps, Tanganyika Territory. A few specimens were found on a specimen of *Mormyrops* sp. collected in these swamps by members of the East African Fisheries Research Organisation.

Lamproglena monodi Capart

Kafue River, N. Rhodesia. Several specimens were recently collected near Mazabuka from two species of *Serranochromis* by Mr D. Harding.

Chilanga, N. Rhodesia. Several specimens were sent to me from fish ponds at Chilanga by Mr M. A. E. Mortimer who found them on specimens of *Tilapia macrochir* Boulenger. The original stock of fish came from the Kafue River.

Malagarasi Swamps, Tanganyika Territory. A few specimens were found on *Tilapia nilotica* (L.) collected in the Malagrasi Swamps by members of the East African Fisheries Research Organisation.

Lake Albert. A few specimens were found on some young *Tilapia* sp. collected in L. Albert by members of the East African Fisheries Research Organisation.

Lamproglena hemprichii Hartmann

Middle Zambezi. I collected a few specimens of this species from specimens of *Hydrocyon lineatus* Bleeker, captured in the Zambezi River near Chiboboma. This is the first record of this species from the Zambezi system.

SUMMARY

Two new parasitic crustaceans of African freshwater fishes are described. These are the copepod *Ergasilus latus*, from L. Rudolf, and the branchiuran. *Chonopeltis flaccifrons* from various parts of the Congo system.

A description of the true male of *Argulus ambloplites* is given, and in the light of its structure it is suggested that *A. jollymani* is best regarded as a sub-species of *A. ambloplites*.

The male of *Argulus dartvellei* is described for the first time.

Notes of the specimens of *Chonopeltis* recorded from the Uelé and Okavango

Rivers are given and it is shown that neither can be satisfactorily identified at present.

Keys to the species of *Chonopeltis* are given.

Some recently established distribution records of parasitic crustaceans of African freshwater fishes are listed.

ACKNOWLEDGMENTS

I am grateful to those persons mentioned in the text who have collected specimens for me or who have lent me material, and would like to mention in particular Mr P. I. R. Maclaren whose tragic death as a result of an encounter with a crocodile has been such a loss to his department in Northern Rhodesia.

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NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

13th October 1959

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.,
President, in the Chair.

"HORMONES IN FISH": A SYMPOSIUM

The following communications were read and discussed :—

Dr R. MORRIS. General problems of osmoregulation with special reference to cyclostomes.

Professor I. CHESTER JONES and J. G. PHILLIPS. Adrenocosteroids in fish.

Dr B. BAGGERMAN. Factors in the diadromus migrations of fish.

Dr U. D'ANCONA. The life-cycle of the Atlantic eel.

Dr J. M. DODD, P. J. EVENNETT and C. K. GODDARD. Reproductive endocrinology in cyclostomes and elasmobranches.

Dr J. BALL. Reproduction in female bony fish.

Dr A. J. MARSHALL. Reproduction in male bony fish.

Professor E. C. AMOROSO. Viviparity in fish.

The above papers will be published in the "Symposia of the Zoological Society of London" Number 1.

10th November, 1959

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.,
President, in the Chair.

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE: JUNE, JULY, AUGUST, SEPTEMBER AND OCTOBER, 1959

By L. HARRISON MATTHEWS, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the months of June, July, August, September and October were 635 in number, including some domestic animals. The following are of special interest :—Five Petz's conures *Aratinga canicularis canicularis*, five Tovi parrakeets *Brotogeris jugularis jugularis*, three Guatemalan parrots *Amazona farinosa guatemalae*, three Yellow-fronted parrots *Amazona ochrocephala* and four White-browed parrots *Amazona albifrons*, presented by Mr W. H. Chippendale, C.M.Z.S.; a Jameson's mamba *Dendroaspis jamesoni* (Traill

presented by Mr. H. A. Revell and two Snouted night vipers *Causus defilippi* (Jan) presented by Mr C. J. P. Ionides, C.M.Z.S., all new to the Collection ; an Azara's douroucouli *Aotes trivirgatus azarae* presented by Mr David Attenborough. The same animal was held on deposit for a short time during 1958. A collection of South American birds including a Black-headed aracari *Pteroglossus viridus viridis* (Linné) new to the Collection, presented by Messrs G. H. and J. R. Newmark ; a jaguarondi *Felis yaguaroundi* presented by Mr N. Pelham Wright ; a pair of emus *Dromiceius n. hollandiae* presented by the Australian Canned Fruits Board ; an Indonesian gibbon *Hylobates moloch* presented by Mr D. J. Henderson ; a Chinese pond heron *Ardeola bacchus* (Bonaparte), an Indonesian gibbon *Hylobates moloch*, two Malayan palm civets *Paradoxurus hermaphroditus musanga*, a Chinese ferret badger *Melogale moschata*, a Pygmy flying squirrel *Petaurillus hosei* (Thomas), a Pallas's squirrel *Callosciurus erythraeus*, a Prevost's squirrel *Callosciurus prevosti* and two Bornean argus pheasants *Argusianus argus grayi* presented by Dr K. C. Searle, C.M.Z.S. The Pygmy flying squirrel and the Chinese pond heron are new to the Collection and the ferret badger does not appear to have been represented in the Collection since the arrival of the first specimen in 1874 ; three Little spider-hunters *Arachnothera longirostris buttikoferi* van Oort, a Yellow-throated flowerpecker *Anaimos maculatus maculatus* (Temminck), a White-breasted wood swallow *Artamus leucorhynchus leucorhynchus* (Linné), two White-crowned shamas *Copsychus malabaricus stricklandi* Motley & Dillwyn, a Black-headed bulbul *Pycnonotus atriceps atriceps* (Temminck) and three Chestnut-breasted tree partridges *Arborophila charltoni graydoni* (Sharpe & Chubb) presented by Mr D. Brameld and Dr K. C. Searle, C.M.Z.S. All these are new to the collection and a Green broadbill *Calyptomena viridis* is the first member of this species to be exhibited since 1931 ; a young male Giant armadillo *Priodontes gigas* G. Cuvier, two Great grey tinamous *Tinamus tao* Temminck, two Banded skinks *Scincus fasciatus* (Peters) [all new to the Collection], a male Malay tapir *Tapirus indicus*, and a female cock-of-the-rock *Rupicola rupicola* were purchased. A female puma *Felis concolor* was purchased as a possible mate for the male " Sabre ". A collection of birds including two Trinidad spectacled owls *Pulsatrix perspicillata trinitatis* Bangs and Penard and an Antillean black hawk *Buteogallus anthracina cancrivora* Clark, new to the Collection, were received in exchange from The Zoological Society of Trinidad and Tobago. One male and two female Viet Nam pot-bellied pigs were received in exchange from the East Berlin Zoo. They were held in Cologne for some time during which one of the females gave birth to five young. Soon after arrival the other female farrowed and five young were born. A Sierra parrakeet *Amoropsittaca aymara* (d'Orbigny) new to the Collection, a lammergeyer *Gypaetus barbatus aureus* and a pair of banteng *Bibos javanicus* were received in exchange. After their statutory quarantine period the banteng will be sent to Whipsnade. A Striped skunk *Mephitis mephitis*, two Collared peccaries *Tayassu tajacu* and a Short-headed flying phalanger *Petaurus breviceps* were born in the Menagerie. Two Spotted eagle owls *Bubo africanus* and two Great house geckoes *Gekko gecko* were hatched in the Menagerie. A red Shining parrakeet *Prosopeia tabuensis splendens* was

A. B.

Mesogastric viscera of *Ateles paniscus*.
A. Stomach in ventral view.
B. Duodenum and adnexa from the dorsal side.

deposited by Mr P. H. Maxwell. During the same period there were 282 additions to the Menagerie at Whipsnade Park including some domestic animals and apart from transfers from London. The following are of special interest :— A Lesser mouse lemur *Microcebus murinus*, presented by Mr Venables ; twenty Grevy's zebras *Equus grevyi*, purchased ; two Saddle-billed storks *Ephippiorhynchus senegalensis*, received in exchange ; two tigers *Panthera tigris* and a giraffe, *Giraffa camelopardalis*, born in the Park ; two Yellow-headed conures *Aratinga jandaya*, a red-rumped parrakeet, *Psephotus haematonotus*, four cockatiels *Nymphicus hollandicus* and three Barraband's parrakeets *Polytelis swainsoni*, hatched in the Park.

The following communications were read and discussed :—

DR W. C. OSMAN HILL. MESOGASTRIC VISCERA IN *Ateles* (SPIDER-MONKEYS) (PLATE 1)

Spider monkeys are unique among Neotropical Primates in their body proportions which, in many ways, parallel developments in Old World forms, more particularly the orthograde apes. It is, therefore, surprising to find that, in respect of the conformation of the mesogastric viscera (with the exception of certain features in the liver), an opposite trend is expressed. The thorax and abdomen are axially shortened and broadened transversely, lumbar vertebrae in particular being reduced to four.

Axial lengthening affects especially the stomach and duodenum. A long thin stomach is briefly mentioned by Murie (1865) in *A. cucullatus* (=*A. geoffroyi grisescens*) and *A. belzebuth*, who draws particular attention to the rounded cardiac end and narrow elongated pyloric region. *In situ* typically the organ forms an elongated U or V with both limbs tube-like, varying in girth according to degree of filling. The fundus is rounded ; the pyloric limb slightly shorter than the proximal limb. In consequence the lesser omentum is provided with a long attachment and terminates caudally acutely at the incisura angularis. The overall picture recalls that of the Dermoptera and *Pteropus*, suggesting thus a predominantly vegetarian diet.

From the pylorus the duodenum at first turns dorsally but rapidly bends caudally in the form of a U-shaped loop with a long proximal, and shorter aboral limb joined by a short transverse segment. The latter is located opposite the third lumbar vertebra while the duodeno-jejunal flexure is level with the second lumbar body.

Perhaps the most remarkable feature is the migration of the termination of the bile and pancreatic ducts to an aboral situation, on the caudal limb of the duodenum. In this *Ateles* agrees with *Lagothrix* and has been previously very briefly noted by van Balen Blanken (1912). Typically in Platyrrhini (e.g. in *Cebus*, *Saimiri*, *Alouatta*) bile and pancreatic ducts open by a common aperture about 1 cm. beyond the pylorus. In *Ateles* the common bile duct, after descending in the lesser omentum crosses the pylorus and courses within the duodenal loop parallel to the proximal limb, more or less masked by pancreatic lobules. Distally it turns leftwards and opens into the duodenum near the duodeno-jejunal flexure. The termination is marked by a prominent oval protrusion of the duodenal wall externally resembling a diverticulum or ampulla, but

relatively solid in structure. The common duct terminates on the ventral side of the apex of this structure which points in an oral direction. Opposite this prominence on the internal surface of the duodenum is the equally prominent duodenal papilla, the two together having a diameter of 1 cm. The ampulla proper is contained within the papilla ; it finally opens on the aboral side of the summit of the papilla the stream of bile being thereby directed aborally. Axially the papilla measures 8·7 mm., transversely 6 mm. and in height 4 mm.

The pancreatic duct after draining the " body " of the pancreas makes a right-angled bend when it meets the bile duct, which it afterwards accompanies in a slightly ventral position and somewhat to the right. It unites with the bile duct just prior to the termination of the latter in the above-mentioned prominence. At the site of the right-angled bend the pancreatic duct enlarges and receives a large sagittally-directed tributary draining the omental lobules of the gland.

An anomalous vascular feature affects the duodenal loop—viz., the failure of the superior and inferior pancreatico-duodenal arteries to meet in the form of an arcade.

Acknowledgment is due to Professor G. Romanes of Edinburgh for the loan of van Balen Blanken's publication (1912).

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Dr L. ADAMSON, Professor R. G. HARRISON and Mrs IRIS BAYLEY. The development of the whistling frog *Eleutherodactylus martinicensis* of Barbados. [To be published in the " Proceedings " Vol. 133, Part 3].

Dr D. M. ROSS. The association between the hermit crab *Eupagurus bernhardus* and the sea anemone *Calliactis parasitica*. [To be published in the " Proceedings " Vol. 134, Part 1].

Dr A. J. MARSHALL. A zoological collector in northwestern Australia. [Illustrated by a coloured film].

8th December 1959

Sir LANDSBOROUGH THOMSON, C.B., O.B.E., D.Sc.,
President, in the Chair.

" CYCLICAL ACTIVITY IN ENDOCRINE SYSTEMS " : A SYMPOSIUM

The following communications were read and discussed :—

Dr A. J. MATTY. Thyroid cycles in fish.

Dr D. R. SWIFT. Cyclical activity of the thyroid gland of the trout in relation to environmental changes.

Dr P. G. W. VAN OORDT. The influence of internal and external factors in the regulation of the spermatogenetic cycle in Amphibia.

Dr A. J. MARSHALL. The environment, cyclical reproductive activity and behaviour in birds.

Professor E. J. W. BARRINGTON. Some problems of adenohypophysial relationships in cyclostomes and fish.

Dr M. J. WELLS. Optic glands and the ovary of *Octopus*.

Dr D. B. CARLISLE. Moulting cycles in Crustacea.

General discussion, with concluding remarks by Professor SIR SOLLY ZUCKERMAN, C.B., F.R.S.

The above papers will be published in the " Symposia of the Zoological Society of London " Number 2.

H. GORVETT and J. C. TAYLOR. A FURTHER NOTE ON TEGUMENTAL GLANDS IN WOODLICE.

In a paper published in this journal a few years ago (Gorvett, 1956), it was shown that the function of the lobed tegumental glands in woodlice is probably defence against attack by spiders. Recent work by one of us (J. C. T.) on certain aspects of the behaviour of ants and their commensals has produced evidence that both supports and extends this view.

Among the animals investigated is the small blind woodlouse *Platyarthrus hoffmannseggi* Brandt. This lives commensally in ants' nests and is apparently never found apart from ants. It occurs in the nests of several different species and is widely distributed. Most observers have claimed that " the ants never pay the slightest attention to this little creature " (Donisthorpe, 1927). But although this may be true of ants and woodlice living in the same nest, ants appear to react very differently to woodlice from elsewhere.

In the course of the investigation mentioned above, experiments were performed to determine how worker ants of the species *Lasius flavus* (Fabricius) behave when (1) other ants of the same species, and (2) commensal animals, are introduced from another nest. It was found that the workers attack *all* intruders, commensals as well as ants. But it is the counter-reaction of the intruding *Platyarthrus* that is especially interesting in relation to the work on lobed glands.

As soon as it is approached by an investigating ant the woodlouse " clamps down ", just as many other woodlice do when disturbed. In *Platyarthrus*, however, the reaction appears to be induced by even the light touch of the ant's antennae, and it is accompanied by a bending upwards of the exopodites of the uropods. The uropods and antennae are now the only parts of the woodlouse accessible to the jaws of the ant. If the ant tries to bite the raised uropod, it is soon evident that its jaws and other mouth-parts have become entangled with the viscous secretion from the uropod glands, for the ant backs away and rubs its head in the nest soil, or wipes its head with its forelegs, apparently trying to clean off the sticky material. If, on the other hand, the ant grasps the woodlouse by its antenna (which contains no lobed glands) it shows no

sign of being repelled and continues to attack. It is uncertain whether the uropod glands begin to secrete after the first light contact with the ant, or only when the uropods are bitten, but previous experimental work on other woodlice (Gorvett, 1956) suggests that the latter is the more probable alternative.

Although the lateral plates also contain lobed glands that, in most woodlice, act in conjunction with the uropod glands, no secretion was detected on the lateral plates of *Platyarthrus*. This may be because the lateral plate glands are poorly developed in this genus : there is only one small gland in each lateral plate, and that only in three segments (Gorvett, 1951). But even in *Porcellio*, where the lateral plate glands are larger and much more numerous, stimulation that usually produces a reaction in both types of gland sometimes results in secretion from the uropod glands alone.

An interesting parallel with the *Platyarthrus* reaction is provided by the behaviour of certain staphylinid beetles (such as *Lomechusa* and *Atemeles*) which also live in ants' nests, and which have a gland with a reservoir opening beneath the abdomen. When attacked, the beetle raises its abdomen and squirts a secretion that " smells of amyl acetate " over the ant and stupefies it (Caullery, 1952, describing work by Jordan, 1913). As in woodlice, the gland is also found in related forms that are not myrmecophilous.

These new observations affect the original hypothesis in two ways. First they provide a convincing piece of additional evidence in support of the principle that the function of the lobed glands is defence. Previously, secretion had been seen to occur under natural conditions only in one kind of situation—that in which a woodlouse is dropped on to a spider's web and the spider allowed to attack it. The introduction of *Platyarthrus* into a strange ants' nest also produces a situation that approximates to natural conditions, and the reaction of the lobed glands to an attacking ant in the field provides more convincing evidence of their defensive function than a similar reaction to experimental stimulation in the laboratory.

The second effect of these observations is to extend the application of the defence hyopthesis by showing that, at least in the case of *Platyarthrus hoffmannseggi*, the glands may be used for defence against ants as well as, or perhaps instead of, against spiders. Herold (1913) suggested that the glands may be poorly developed in *Platyarthrus* because it is protected by ants, while Bristowe (1941) stated that *Platyarthrus* is less distasteful to spiders than certain other woodlice because " its myrmecophile habit renders it less likely to attack by spiders ". In fact, it would seem that, because of its small size and specialised mode of life, *Platyarthrus* is more liable to attack by ants than by spiders. And since ants, like spiders, attack by means of biting jaws, they probably provide the same stimulus as spiders do to the glands, and their mouth-parts are probably affected in the same way as those of spiders by the viscous secretion, So it seems unlikely that any modification of the glands would be needed to enable them to be used in *Platyarthrus* for defence against ants.

The lobed glands may perhaps be used occasionally by other woodlice besides *Platyarthrus* to ward off ants, and possibly other biting arthropods

such as centipedes (although experimental evidence suggests that *Lithobius* does not find the lobed gland secretions distasteful). But it still seems probable that, for most woodlice, the spider is by far the most important predator, and that it is to repel spiders that the lobed gland system was primarily evolved.

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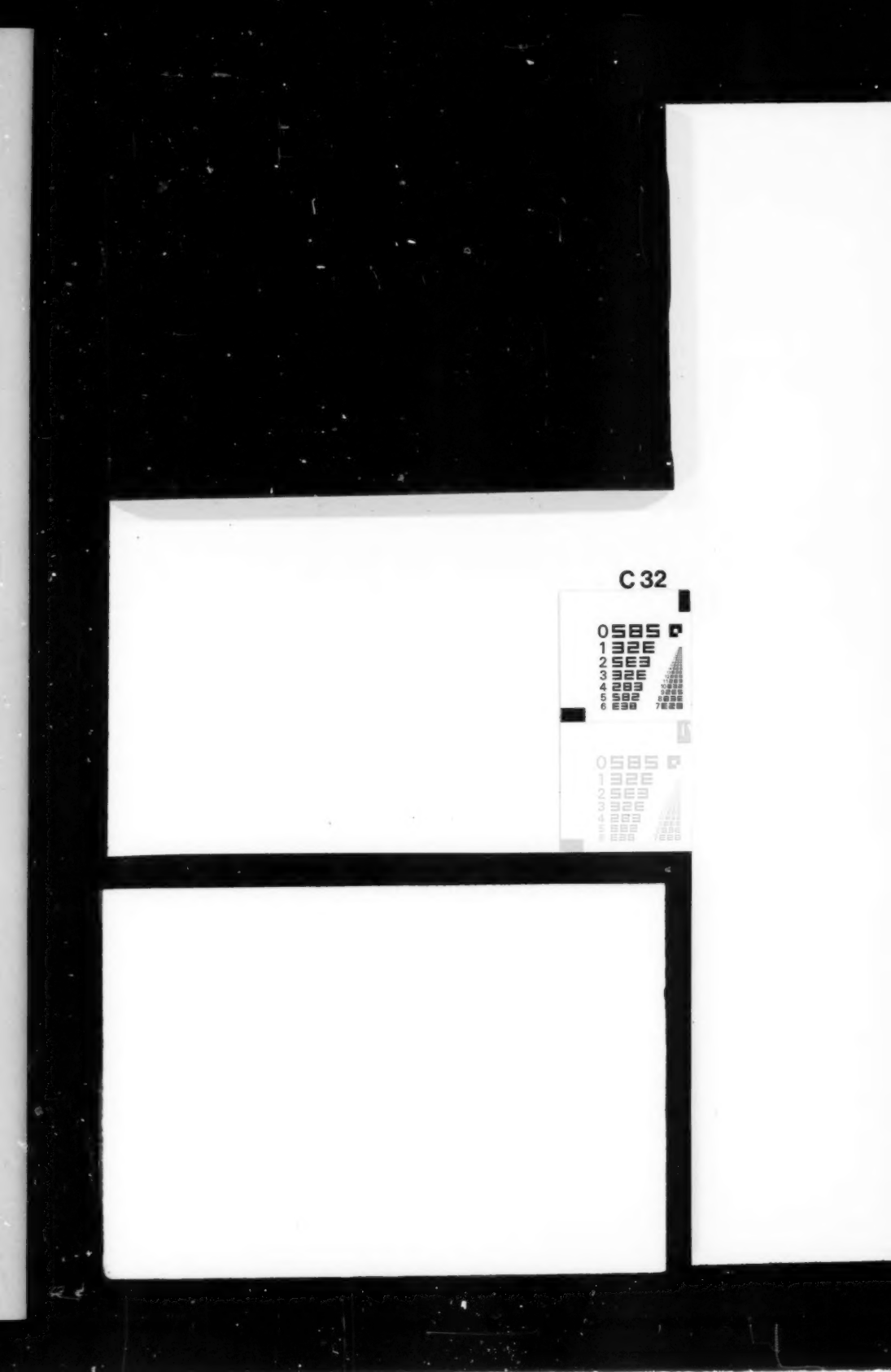
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